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SYNOPSIS OF BIOLOGICAL DATA ON *Laminaria hyperborea*

Prepared by

Joanna M. Kain

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no. 87

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
ROME, 1971

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SYNOPSIS OF BIOLOGICAL DATA

ON Laminaria hyperborea

Prepared by

JOANNA M. KAIN (Mrs. N.S. JONES)

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FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
Rome, December 1971

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PREPARATION OF THIS SYNOPSIS

Laminaria hyperborea has been, for a long time, one of the seaweed species of greatest industrial importance in Scotland and other parts of the northeastern Atlantic. Also, much of the pioneer work on seaweed biology and chemistry was done on this species. Therefore, a review of the information available on the species was considered to be particularly valuable for all those concerned with seaweed research and utilization.

This synopsis has been edited by G. Michanek, of the Marine Biology and Environment Branch, Fishery Resources Division, FAO.

The author is extremely grateful to Dr. A. Jensen (Norway) who very kindly allowed her to use his own drafts of the sections on harvesting, chemistry and utilization, thereby providing a more authoritative basis and saving her much time.

Many people have been very helpful in providing information. For this the author is much indebted in particular to Dr. K. LÜning (Germany, FRG), Cand. real P. Svendsen (Norway), Mr. E. Booth, Dr. J.W.G. Lund and Mr. H.T. Powell (U.K.), Dr. A.H. Dizerbo (France), Professor J. Seoane-Camba (Spain), Dr. Y. Hasegawa and Dr. S. Kawashima (Japan), Dr. G. Michanek (Sweden) and Cand. real S. Sivertsen (Norway). She is also very grateful to the following for permission to quote unpublished data: Cand. real P. Svendsen, Mr. A. Whittick (Canada), Dr. D.M. John (Ghana) and Cand. real O. Vahl (Norway). For permission to reproduce published figures she is indebted to Dr. K. LÜning, Cambridge University Press, Professor E. Baardseth (Norway), the Norwegian Institute of Seaweed Research and the Marine Biological Association of the United Kingdom.

In the text depths are expressed in metres below the lowest astronomical tide (LAT) which is defined as "the lowest level which can be predicted to occur under average meteorological conditions and under any combination of astronomical conditions" (U.K., Admiralty, 1963). Where necessary depth data have been corrected, usually to the nearest metre, from the relevant tidal data.

Where possible, algal names have followed the latest British check-list (Parke and Dixon, 1968) and animal names have followed the Marine Fauna of the Isle of Man (Bruce et al., 1963).

Distribution:

FAO Department of Fisheries
FAO Regional Fisheries Officers
Regional Fisheries Councils and Commissions
Selector SM
Author

Bibliographic entry:

Kain, J.M. (1971)
FAO Fish.Synop., (87):pag.var.
Synopsis of biological data on Laminaria hyperborea

ANE. Laminariaceae. Taxonomy, morphology and anatomy. Distribution, ecology, metabolism and growth. Life cycle, reproduction, phenology. Population - structure, density and standing crop. Harvesting - techniques, seasons, yields. Chemical composition. Utilization. Selected bibliography.

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1 IDENTITY

1.1 Nomenclature

1.11 Valid scientific name

Laminaria hyperborea (Gunnerus) Foslie.

This was described and figured by Gunnerus (1766) as Fucus hyperboreus, but recombined as Laminaria hyperborea by Foslie (1885).

1.12 Nomenclatural synonyms

Many synonyms are given by Foslie (1885), De-Toni (1895), Du Rietz (1920, 1953) and others, the most important being the following:

Fucus scoparius Strøm, 1762
Fucus digitatus Mohr, 1786
Laminaria digitata Lyngbye, 1819
Laminaria phycodendron la Pylaie, 1824
Hafgygia digitata Kützing, 1843
Laminaria cloustoni Edmondston, 1845
Hafgygia cloustoni Areschoug, 1883
Laminaria digitata f. typica Foslie 1884

The earlier name Fucus scoparius of Strøm (1762) was invalid because, although it clearly applied only to this species, it was published in a work not generally employing binary nomenclature (Du Rietz, 1953).

For many years there was confusion between this species and L. digitata (Huds.) Lamour., e.g. by Lyngbye (1819), and Harvey (1846-51) and although Le Jolis (1855) clearly distinguished the two species and listed their reliable characters some confusion continued and even Foslie (1884, 1885) misidentified some specimens (Munda, 1965). He (Foslie, 1885) was satisfied, however, that Gunnerus (1766) had not included L. digitata in his description because he examined Gunnerus' herbarium including the type specimen. Unfortunately Le Jolis (1855) had not been of this opinion and thought that Gunnerus' description was thus invalid, and that Edmondston's L. cloustoni was therefore the first valid name. This synonym was used for many years, particularly in Britain (e.g. Newton, 1931).

1.13 Vernacular names

Norway: Trolltare, stortare, stokktare, palmetare, skrame, hestatare, havtare, kurvtare, stolpetare (Grenager, 1953).

British Isles: Tangle, redware, cuvie, cuvy.

Germany: Palmentang.

France (Brittany): Tali-penn, tali-ebrel.

Ohmi (1968) gives 22 names for the species, most of which are in very local use if at all.

1.2 Taxonomy

1.21 Affinities

- Suprageneric

Laminaria hyperborea (Gunn.) Fosl. belongs to the family Laminariaceae of the order Laminariales of the division Phaeophyta.

- Generic

The genus Laminaria was set up by Lamouroux (1813) with L. digitata as the type species. The following is a diagnosis of the genus.

The sporophyte is in three distinct parts, holdfast, stipe and frond (lamina or blade). The holdfast may be a disc or more commonly formed of branched haptera which in a few species give rise to more than one stipe. The stipe is simple (occasionally branched following damage), terete or flattened, and expanded into a smooth frond which may be entire or split into segments distally. The primary growth region is the transition zone between stipe and frond. The frond has no midrib but may be elevated or depressed in different areas. It has no cryptostomata or natural perforations. Mucilage ducts may be absent from the plant or present in the frond and sometimes also in the stipe. Unilocular sporangia are borne in irregular dark-coloured sori on the frond. The zoospores develop into microscopic sexual dioecious gametophytes, each female unicellular or a simple or branched filament, each male multicellular but varying also in complexity.

The genus is usually divided into two sections, the Simplices with an undivided frond, the Digitatae with the frond normally split into segments. Well over a hundred species of Laminaria have been described but the majority of these names are invalid, having been transferred to other genera or being synonyms of valid specific names. There remains considerable confusion about many of the specific names still in use. This is mainly because many species are morphologically plastic and only recently have serious attempts been made to define specific boundaries by experimentation. There is confusion both within small geographical areas where perhaps a few species show many forms erroneously termed species and between widely separated areas where perhaps the same specific epithet is used for differing entities. In view of the taxonomic chaos in which the genus must be considered to be, the following list must be considered as a guide only. Much more research must precede a definitive list of species. The Simplices section is discussed in more detail by Burrows (in preparation).

Species of the genus Laminaria are listed below in approximate order of geographical distribution, starting with those occurring in the Northeast Atlantic and progressing westward.

L. hyperborea (Gunn.) Fosl. Distinct species. Northeast Atlantic.

L. digitata (Huds.) Lamour. Distinct species with several varieties or forms induced by habitat. Northeast and Northwest Atlantic, Arctic.

L. gunneri Fosl. Indistinct species of local occurrence. North Norway.

L. ochroleuca la Pylaie. Distinct species. Northeast Atlantic.

L. pallida (Grev.) J. Ag. Distinct species. Southeast Atlantic, Southern Ocean.

L. schinzii Fosl. Somewhat doubtful species, of local occurrence. South Africa.

L. rodriguezii Bornet. Distinct species. Mediterranean.

L. saccharina (L.) Lamour. This and the next two species are only distinguishable by the presence or absence of mucilage ducts in the stipe and frond. Wilce (1965) aggregates them as L. saccharina but as at least one is genetically distinct (Burrows, 1964) the species delimitation is uncertain. Northeast and Northwest Atlantic, Arctic, Northeast and possibly Northwest Pacific.

L. groenlandica Rosenv. See notes on L. saccharina. Arctic, Northwest Atlantic, Northeast Pacific.

L. agardhii Kjellm. See notes on L. saccharina. Northwest Atlantic.

L. atrofulva J. Ag. Doubtful species of local occurrence. West Greenland.

L. nigripes J. Ag. Thought to be distinct by some authors but Wilce (1965) suggested synonymy with L. digitata. Arctic, Northwest Atlantic.

L. longicruris la Pylaie. Probably a distinct species though there has been doubt about mucilage ducts. Northwest Atlantic.

L. faeroensis Borgesen. Doubtful species because its difference from L. longicruris is based on mucilage ducts about which there is uncertainty. Northeast Atlantic.

L. solidungula J. Ag. Distinct species. Northwest Atlantic.

L. cuneifolia J. Ag. Doubtful species. According to Wilce (1959) this name is invalid and the plants attributed to it indistinguishable from L. groenlandica (Wilce, 1965) but Druehl (1968) retains the species. Northwest Atlantic, Northeast Pacific.

L. platymeris la Pylaie. Doubtful species. This is variously regarded as digitate or simple and included in L. groenlandica by Druehl (1968) and in L. digitata by South and Cardinal (1970). Northwest Atlantic, Northeast and Northwest Pacific.

L. fissilis J. Ag. Doubtful species. Northeast Pacific.

L. bongardiana Post. et Rupr. Doubtful species. Northeast Pacific.

L. sinclairii (Harv.) Farl. Distinct species. Northeast Pacific.

L. ephemera Setch. Distinct species. Northeast Pacific.

L. farlowii Setchell. Possibly a distinct species but of local occurrence. Northeast Pacific.

L. complanata (Setch. et Gardn.) Setchell. Probably a distinct species. Northeast Pacific.

L. setchellii Silva. Distinct species. Northeast Pacific.

L. ruprechtii (Aresch.) de Toni. Local occurrence. Alaska.

L. dentigera Kjellm. Possibly a distinct species. Northeast and Northwest Pacific.

L. longipes Bory. Distinct species. Northeast and Northwest Pacific.

L. yezoensis Miyabe. Variable species. Northeast and Northwest Pacific.

L. ensiformis J. Ag. Doubtful species of local occurrence. Northwest Pacific.

L. japonica Aresch. This and the following three species were shown by Yabu (1964) to be interfertile. Some are geographically separated and may be ecads (Hasegawa, 1966). However, as transplantation experiments have not been reported it is not known at present whether they are genetically distinct.

L. religiosa Miyabe. See notes on L. japonica. Northwest Pacific.

L. ochotensis Miyabe. See notes on L. japonica. Northwest Pacific.

L. diabolica Miyabe. See notes on L. japonica. Northwest Pacific.

L. fragilis Miyabe. Doubtful species of local occurrence. Japan.

L. longipedalis Okam. Somewhat doubtful species of local occurrence included in L. diabolica by Miyabe and Nagai (1933) and separated by Miyabe (1902, 1936). Japan.

L. cichorioides Miyabe. Distinct species. Northwest Pacific.

L. angustata Kjellm. Distinct species. Northwest Pacific.

L. coriacea Miyabe. Distinct species. Northwest Pacific.

L. sachalinensis Miyabe. Probably a distinct species. Northwest Pacific.

L. sikotanensis Miyabe et Nagai. Local occurrence. Northwest Pacific.

L. yendoana Miyabe. Probably a distinct species but of very local occurrence. Japan.

L. subsimplex Miyabe et Nagai. Doubtful species included in L. cuneifolia by Setchell and Gardner (1925) but retained by Nagai (1940). Northwest Pacific.

L. taeniata Post. et Rupr. Doubtful species. Northwest Pacific.

L. palmaeformis Okam. Probably a distinct species. Northwest Pacific.

L. gurjanovae A. Zin. Distinct species recently described. Northwest Pacific.

- Specific

Gunnerus' herbarium is in Trondheim Museum but the type specimen of Laminaria hyperborea appears to be lost.

Diagnosis of L. hyperborea:

Stipe terete, thicker near the base, rugose except in young plants or new growth, rigid, containing mucilage ducts. Very young stipes of 1-20 cm distinguishable from L. digitata by a narrowing at the transition zone. Frond developing from November onward separated from old frond by a narrow collar after the first year. Sorus covering most of old frond for 1-2 months between September and April. Tissue positive to benzidine test (Jensen and Haug, 1952).

Note on the benzidine test:

Two solutions are prepared; A. 5 g benzidine, 25 ml 25 percent HCl, to 1 000 ml with H_2O; B. 10 g $NaNO_2$, to 100 ml with H_2O. Equal quantities of A and B are mixed five minutes before use and used for up to two hours. Freshly cut tissue of L. hyperborea (and of some other algae) turns bright red immediately on application. That of L. digitata changes to yellow-brown slowly.

CAUTION: Users should be well protected from benzidine because it is highly carcinogenic and can pass through skin.

Specimens of L. hyperborea are deposited at the British Museum (Natural History), Cromwell Road, London S.W.7.

The following key has to rely largely on the presence or absence of mucilage canals as distinguishing characters. These may not be very reliable and are often difficult to see. Many of the species of Laminaria must be treated with caution, as explained earlier. All the very doubtful species and those of very local occurrence are omitted.

1.	Frond normally digitate (splits may fail to appear in very calm water)	2
	Frond entire	11
2.	Holdfast a disc	3
	Holdfast formed of haptera	5
3.	No mucilage ducts in frond or stipe, sori elongated	L. ephemera
	Mucilage ducts in frond but not stipe	4
4.	Stipe terete but thicker near the base, warty outgrowths on stipe and holdfast when old	L. yezoensis
	Stipe flattened distally, lamina deeply split	L. palmaeformis
5.	Stipe terete but thicker near the base, tapering just above haptera, with mucilage ducts	6
	Stipe cylindrical at base, terete or flattened distally, with or without mucilage ducts	8
6.	Stipe rugose except when young, rigid, mucilage ducts present	L. hyperborea
	Stipe smooth	7
7.	Frond dark, occurs in Pacific	L. dentigera
	Stipe and frond light in colour, occurs in Northwest Atlantic	L. ochroleuca

8. Stipe light in colour, terete, occurs in South Atlantic — L. pallida
   Stipe dark, may be flattened distally, smooth or rugose — 9

9. Stipe smooth and flexuose, devoid of mucilage ducts which are present in frond — L. digitata
   Mucilage ducts present in stipe — 10

10. Mucilage ducts near surface of stipe, stipe nearly black, smooth flattened distally — L. nigripes
    Mucilage ducts in mid-cortex of stipe, stipe smooth, flattened distally — L. setchellii

11. Stipe hollow — L. longicruris
    Stipe solid — 12

12. Holdfast a disc — 13
    Holdfast of haptera — 15

13. No mucilage ducts in either frond or stipe, sori elongated — L. ephemera
    Mucilage ducts in frond — 14

14. No mucilage ducts in stipe, stipe thicker near base, Pacific — L. yezoensis
    Mucilage ducts in stipe, sori rounded, Northwest Atlantic — L. solidungula

15. Haptera giving rise to more than one stipe (rhizomatous) — 16
    Single stipe per holdfast — 18

16. Mucilage ducts present in frond, absent from stipe — L. longipes
    Mucilage ducts present in frond and stipe — 17

17. Stipe smooth, occurring in Mediterranean — L. rodriguezii
    Stipe rugose, occurring in Northeast Pacific — L. sinclairii

18. Stipe flat for distal two-thirds of its length — L. complanata
    Stipe mainly terete — 19

19. Occurring in Atlantic, Arctic, Northeast Pacific or Bering Sea — 20
    Occurring in Northwest Pacific only — 22

20. No mucilage ducts in either frond or stipe — L. agardhii
    Mucilage ducts in frond — 21

21. No mucilage ducts in stipe — L. saccharina
    Mucilage ducts present in stipe — L. groenlandica

22. Stipe 2-3 mm in diameter, mucilage ducts in frond but not stipe — L. gurjanovae
    Stipe 4 mm or more in diameter — 23

23. Stipe of mature plant 300-600 mm long, mucilage ducts in both stipe and frond — L. longipedalis
    Stipe less than 300 mm long — 24

24. Median fascia less than a quarter of the width of the frond — L. angustata
    Median fascia more than a quarter of the width of the frond — 25

25. Margins of the frond crispate and waved throughout its length, mucilage ducts in both stipe and frond — L. cichorioides
    Margins of the frond not crispate, and not waved near the transition zone — 26

26. Median fascia more than three-fifths of the width of the frond, coriaceous and rigid, mucilage ducts in frond but not stipe — L. coriacea
    Median fascia less than three-fifths of the width of the frond — 27

27. Mucilage ducts in frond but not stipe — L. saccharina
    Mucilage ducts in both frond and stipe — 28

28. Bullae present on median fascia except in very old fronds, haptera verticillate — L. sachalinensis
    Bullae only present in very young fronds — L. japonica group

1.22 Subspecies

There are no subspecies of L. hyperborea. However, two forms other than f. hyperborea have been described. The first was by Foslie (1885) and was L. hyperborea f. compressa Foslie. This was a renaming of his L. digitata f. longifolia Foslie (Foslie, 1884). The form is figured only as a transverse section of the stipe, which is flattened. As no specimen of this form can be traced in Foslie's herbarium and the strong possibility that this was a form of L. digitata cannot be eliminated, it would seem prudent to ignore the description at present.

The second forma is L. hyperborea f. cucullata Svendsen et Kain and is an ecad characteristic of very calm water (Svendsen and Kain, 1971). It is found in very sheltered areas and in comparatively deep water in slightly exposed areas, mainly in Norway. It is distinguishable from L. digitata f. cucullata Le Jolis which it closely resembles by the taper near the base of the stipe, the collar between the new and old frond and the positive reaction to the benzidine test.

1.23 Genetic data

The chromosome number in young sporophytes, unilocular sporangia and female gametophytes has been counted by Evans (1965). Because of the small and mixed size of the chromosomes the counts were variable but he thought the most likely numbers to be 31 haploid and 62 diploid.

In the north European species of Laminaria it seems that the species boundary coincides with an interfertility barrier. This conclusion is made from Schreiber's (1930) beautiful set of experiments in which he failed to obtain hybrids between L. hyperborea, L. digitata and L. saccharina. On the other hand, Sundene (1958) and Svendsen and Kain (1971) obtained normal sporophytes from crosses of gametophytes from different forms or ecads of L. digitata and L. hyperborea respectively.

Chapman (1948) suggested that differences in the vertical distribution of L. hyperborea with latitude might be attributable to different strains of the species. Kain (1969) grew plants from spores from Norway and the Isle of Man at different irradiances and temperatures and observed almost identical growth. A more likely explanation for Chapman's observation is his alternative suggestion that it is due to differences in ecological conditions.

1.3 Morphology and anatomy

1.31 External morphology

The mature plant is distinctive and well differentiated (Fig. 1). The holdfast consists of haptera which have grown out of the base of the stipe. The stipe base is in the shape of an inverted cone, the lower tip being the point of original attachment but which may not still be in contact with the rock. Around this position there is a ring of small haptera and progressively more recent haptera produced upward from here are arranged in about seven to eight vertical rows, each of up to about ten haptera. Each hapteron is terete, up to about 10 mm in diameter, and is branched about four times, the branches decreasing in diameter. The tips of the haptera are expanded into small discs adhering to the rock. When a holdfast is attacked by the limpet Patina pellucida (L.) the haptera produced nearest to the cavity formed are clearly stimulated in their growth and branching so there is a tendency for the cavity to be covered up and extra attachment to the rock formed.

The stipe is terete for the whole of its length, except where it flattens suddenly into the transition zone distally. It tapers slightly over most of its length but mainly near the base and apex. The mature stipe is sufficiently rigid to bear the weight of the frond out of water with little bending except near the tip but can usually be forcibly bent into a complete circle before snapping and showing a clean break. Except when newly formed, the surface of the stipe is rugose or papillate and is thus a suitable substratum for many epiphytes.

At the transition zone the stipe expands into the frond. The frond is a flat and very smooth blade normally divided into fingers. The shape of the base depends on the habitat but is usually truncate or slightly cordate.

The morphology of the plant is markedly affected by water movement. Where there is strong wave action the holdfast is well developed with thick, well branched haptera and a large area of attachment. The stipe is fairly rigid and more or less straight. The frond is leathery, truncate at the base, fan shaped and divided into many segments, 30 fingers being common. The outer fingers of the new frond (Fig. 1B) are released early (February) and the old frond is often lost in March. With decreasing exposure the number of fingers of the frond decreases and the old frond remains attached until later. Where there is a strong current but little wave action, the holdfast is also well developed but the stipe probably more flexible. The frond is cuneate at the base and fingered but much more elongated than the fan-shaped wave action form. The plant is then similar to L. digitata under similar conditions, particularly in the shape of the frond.

In conditions of shelter from both wave action and water currents, the plant has a very different appearance and is termed f. cucullata. The holdfast is poorly developed with few and weak haptera and weak adhesion to the rock. The stipe is bent or tortuous and short, normally being less than 50 cm. The frond is thin, brittle and easily torn, cordate at the base, entire and broad, forming a draping "apron" (Svendsen and Kain, 1971).

The frond:stipe weight ratio at any given age increases with shelter and with depth (Kain, 1971a).

For the maximum size attained by this species see 4.12.

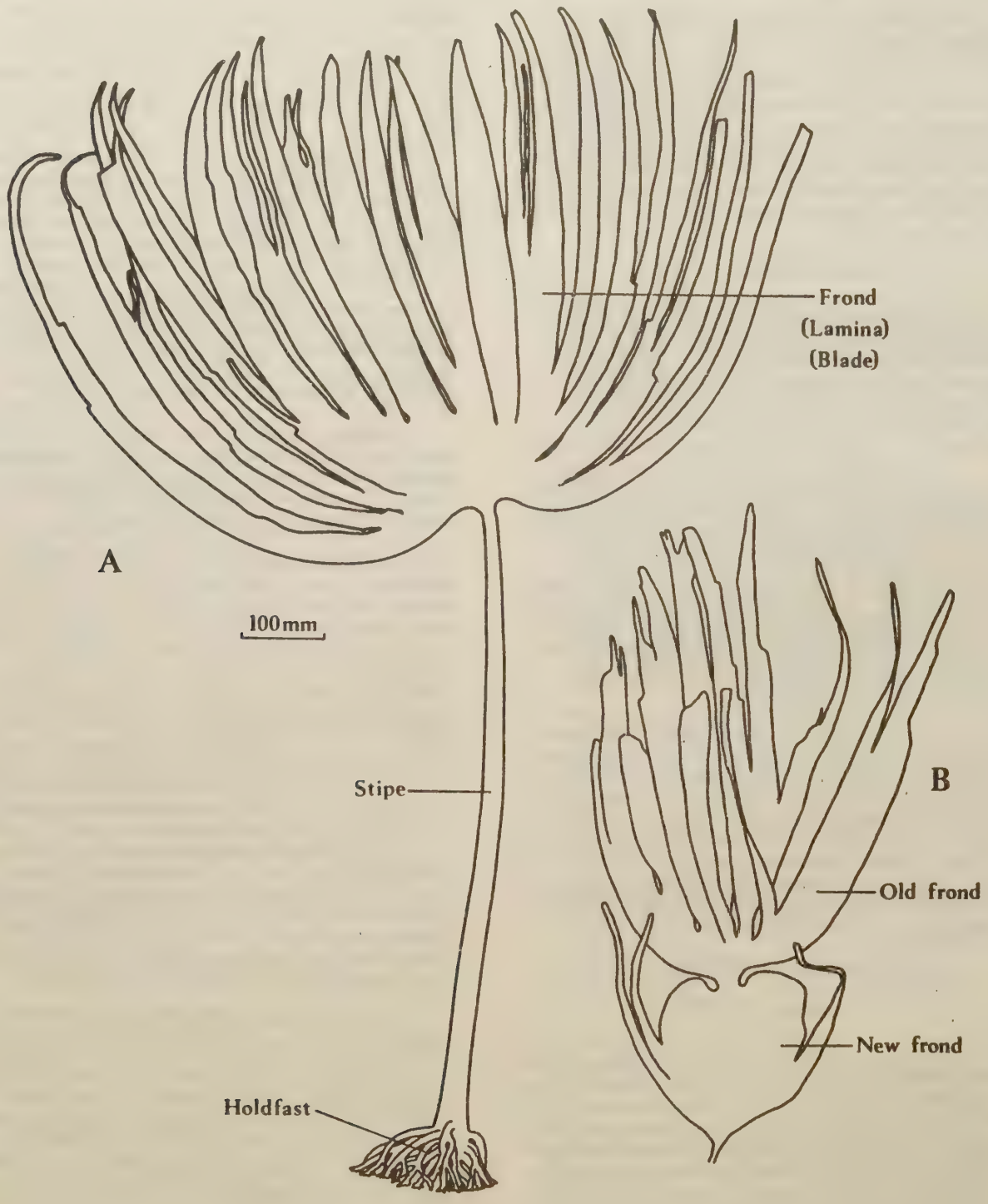


Fig. 1 Drawings of sporophytes of L. hyperborea

A. Whole plant during the slow growing season.

B. Part of a younger plant in February showing old and new fronds.

1.32 Anatomy

Killian (1911) described the anatomy of L. digitata in detail and compared it with that of L. hyperborea.

The mature stipe is differentiated into a number of different tissues. Some originate from primary growth and some from secondary. The transition zone is responsible for primary growth. The activity of this zone results in elongation of the stipe below and production of the frond above. The meristematic tissue is said (e.g. by Killian, 1911) to be confined to the surface layer of cells but these could not by themselves account for all the growth in length so it seems likely that the inner tissues must also divide. The surface meristem, or meristoderm, consists of small cells containing chromatophores and covered by a layer of mucilage. Radial rows of similar cells are cut off centripetally. Passing inward (Fig. 2A) these gradually become wider, elongated and paler in the outer cortex. The cells have pointed ends and are arranged less regularly. Cells of the inner cortex, into which these grade, are longer still, have blunt ends and walls thickened with mucilage. Some of them have small tube-like outgrowths. The cells of the inner and outer cortex show up in different colours under a polarization microscope (Baardseth, 1964). Passing inward the cell rows become more separated from each other by mucilage but in some cases are still joined horizontally by their original pit connexions. In L. digitata and Saccorhiza polyschides (Killian, 1911; Sauvageau, 1918), and therefore probably in L. hyperborea, more numerous horizontal connexions between these filaments are formed by a process with the partial appearance of conjugation. Opposing papillose outgrowths on adjacent filaments grow toward each other and join, with a breakdown of the separating walls but no fusion of nuclei. During growth in length the medullary cells appear only to be produced successively from the inner cortex and they consequently become stretched. As the septa of the original longitudinal cells seem fairly rigid the cell walls in these regions are pulled into a trumpet shape. The swollen ends are filled with granules. At the same time, the cross connexions lengthen and become mainly oblique. In addition to these two types of cells in the medulla, there are later formed the so-called hyphae as outgrowths from cortical cells (Fig. 2A). These become very numerous and grow mainly horizontally through the mucilaginous spaces between the other, thicker, medullary elements. The medulla thus consists of filiform ramified tubes entangled into a felt.

Mucilage ducts of the stipe arise below the transition zone as lenticular spaces between the outermost cells in the outer cortex (Guignard, 1892). As cell division continues on the outside, the spaces appear deeper in the cortex and enlarged, with occasional connexions to the meristoderm. At the inner margin, groups of small cells appear and divide. They form an irregular layer on the inner surface of the duct, have dense contents and are secretory. Secretion of mucilage appears to originate from the Golgi vesicles (Schnepf, 1963). The epidermis of the maturer part of the stipe, well below the transition zone, where the surface is rugose, consists of a brown, fairly thick, cork-like layer (Schultz-Schultzenstein, 1853).

Secondary growth in thickness is accomplished through a secondary meristem situated in the cortex inside the mucilage ducts (Fig. 2A). How the tissues external to the meristem are replenished as the circumference increases, is not clear but the meristoderm may be responsible. The secondary meristem produces cells of the outer cortex only. The medulla of the stipe thus remains the same diameter as is formed by primary growth and is thus wider distally, but the cortex increases annually. During the fast growing season each year, an approximate cylinder of cortical tissue is thus laid down outside the stipe tissue of the previous year. During the slow growing period few cells are laid down and these are darker in colour than fast grown cells. This is apparent to the naked eye but hardly distinguishable microscopically. It results in annual growth rings (in transverse section) or lines (in longitudinal section) (Kain, 1963). The dark line for each year has the same length as the stipe at the time of the slow growing season during which it was formed. Figure 3A shows diagrammatically the slow growth lines of a two-year old plant, the stipe of which was 100 mm long at the end of the first season of fast growth and 330 mm long at the end of the second.

Haptera are produced during the fast growing season. The external cell layers of the stipe divide tangentially and produce a hump in which there is an apical meristem (Killian, 1911). Growth in length continues until the hapteron reaches the rock surface when it expands into an irregular disc. There is no medulla in a hapteron but the internal cells are elongated. Mucilage ducts are present. The epidermal cells have few chromatophores at first, so the hapteron is pale, but more later when the hapteron darkens. Numerous rhizoids grow out from the disc and become attached. If one hapteron ring is formed during each fast growing period, then each hapteron is separated from the next by a slow growth line. Thus tracing each line to the outside between the haptera demonstrates the number of haptera rings formed each year, which varies. The shape of the base of the stipe (Fig. 3B) as an inverted cone is explained by the increase in the thickness of the stipe with each year of secondary growth which extends only down to the last ring of haptera, leaving the

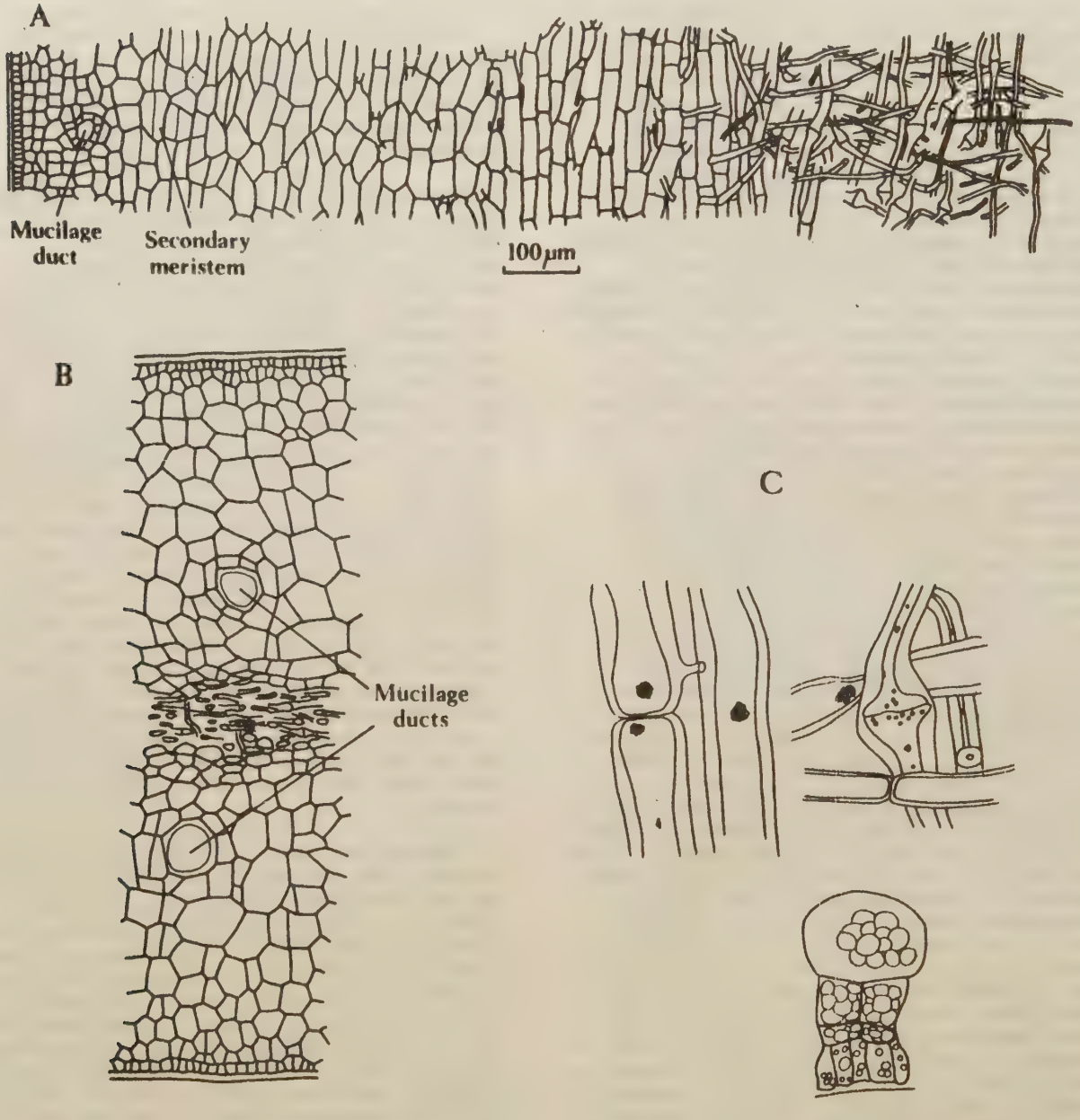


Fig. 2 Anatomical drawings of L. hyperborea

A. Half a longitudinal section of a young stipe.

B. Transverse section of frond (same scale).

C. Physodes in medullary (above) and surface (below) cells (magnification about four times that of A and B), from Baardseth (1958).

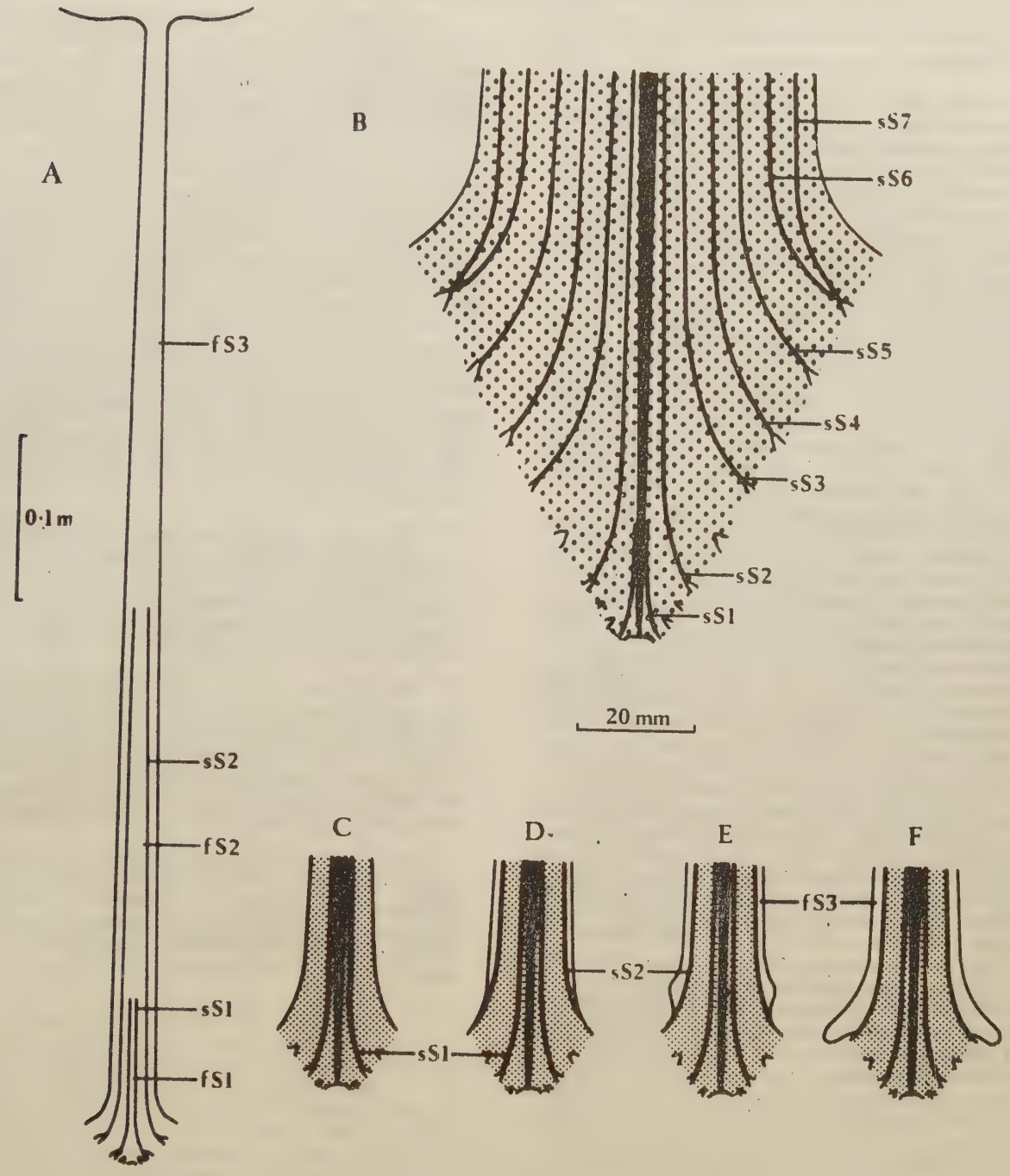


Fig. 3 Diagrammatic representation of slow growth lines in the stipe of L. hyperborea

A. Median transverse section of whole stipe of 2-year old.

B. Median transverse section of the base of 7-year old.

C–F. Similar sections of 2-year olds sampled during the fast growing season. Primary tissue shown black.

fS1, fS2, fS3, fast secondary growth of 1st, 2nd and 3rd years respectively; sS1, sS2, sS3, slow secondary growth of 1st, 2nd and 3rd years respectively.

stipe below only as thick as that of the previous year.

Plants can be aged by observation of the slow growth lines (Kain, 1963). After removing all but a few millimetres of each hapteron, the base of the stipe is cut longitudinally and centrally, passing through a row of haptera. A thick section is then taken. In Figure 3B, which is diagrammatic only, the primary tissue is shown black although in the plant the medulla is more easily distinguished in this region. Near the base the junction of the primary and secondary tissues can appear slightly darker and be confused with a slow growth line. If this turns centripetally when followed down to the base it is the primary/secondary tissue junction, but if it turns outward over the first attachment disc or haptera then it is a slow growth line dating from when the plant was very small. Later lines can be counted more easily (Fig. 3B), particularly if the separation by haptera is noted. A count should be made on both sides. If the plant is sampled during the fast growing season from December to June, care must be taken to determine that the last slow growth line has been made apparent by the current fast growth. If, as in Figure 3C, the last apparent growth line was inside the outer ring of haptera which were clearly dark and rugose and therefore a year old, then there must be another slow growth line not yet visible but which should be counted. If, on the other hand, as in Figure 3D, there are no haptera on the outer side of the last line, then secondary thickening of the stipe has already started and demonstrated the last line, though haptera have not yet developed. These can be seen to be developing in Figure 3E. Finally, when new haptera have developed, as in Figure 3F, the line is again inside a hapteron ring but these haptera can be easily distinguished from those a year old because they are pale and smooth and may not have expanded at their tips. Infestation by Patina pellucida makes age determination difficult firstly because much of the tissue is removed and secondly because "interference" lines and additional haptera are produced as a reaction to the infestation.

The frond is also produced by the activity of the transition zone. It has basically the same structure as the stipe (Fig. 2B), and the meristem, cortex and medulla (but not the mucilage ducts) of the two structures are continuous with each other. Just above the transition zone the lamina is thick but lateral expansion, partly due to anticlinal division of the meristoderm, results finally in a thin blade with a thinner epidermal region than the stipe, a limited number of cortical cell layers and a confused network of medullary elements lacking the mainly longitudinal arrangement of the stipe. There are fewer hyphae than in the stipe. There is some doubt as to whether the medulla cells arise only from the transition zone or also from cortical cells of the frond. The lateral stretching results in the cross connexions in the medulla becoming longer than in the stipe and more cell walls forming across them. When the frond expands and becomes thinner, both medulla and cortex are reduced but the cortex is less reduced than the medulla.

Mucilage ducts in the blade are produced just above the transition zone (Guignard, 1892) and are positioned in the cortex as in the stipe (Fig. 2B). They are spread out in an anastomosing network beneath each surface of the frond, with no connexion between the two systems.

The splits in the frond of L. hyperborea are not accidental tears but are preformed by the activity of the tissues (Killian, 1911). Longitudinal furrows appear in the epidermis on one or both sides of the frond, these deepen and the internal tissues rupture. The epidermis then grows over the edge of the cortex and medulla.

In common with other Phaeophyta, L. hyperborea cells contain vesicles of fucosan, or physodes. The appearance of these in the surface cells and in the medullary elements is shown in Figure 2C (Baardseth, 1958). The latter are apparently more distinctive of the species.

2 DISTRIBUTION, ECOLOGY AND METABOLISM

2.1 Total area

L. hyperborea is confined to the northeast Atlantic (Fig. 4). It was reported absent from Spitzbergen by Svendsen (1959) but more recently Dizerbo (1969) has reported it present from specimens collected by Moign (1965). These have not been checked with the benzidine test and are not typical of L. hyperborea from further south. There is little available information on Jan Mayen or Bear Island. Before Dizerbo's Spitzbergen report the most northern known occurrence was the North Cape in Norway and the plant extends westward along the north Norwegian coast and a short distance into the U.S.S.R. (Vozzhinskaya, personal communication). It also extends south along the rest of the Norwegian coast and along the west coast of Sweden into the Kattegat (Rosenvinge and Lund, 1947). According to Jónsson (1912) it occurs on most of the coast of Iceland except part of the east, being present only at the mouth of Berufjörður. However, Munda (1969) has reported it from Reyðarfjörður, further north into this eastern region affected by the Arctic current. It occurs in the Faeroes (Edmondston, 1845), the Orkneys (Spence, 1918), around most of the British Isles (including the Scilly Isles, Harvey, 1969) and around the Channel Islands (Kain, 1961). It is present in Helgoland but absent from the rest of Germany. There is none on the Dutch coast (Hartog, 1959). It is present on the coast of Normandy (Le Jolis, 1855) and Brittany (Sauvageau, 1918) and southward (Hamel, 1939; Hoek and Donze, 1967) but rare on the Basque (Feldmann and Lami, 1941) coasts of France. It reappears on the north coast of Spain where the temperature is lower (Hoek and Donze, 1966). According to Seoane Camba (1966) its southern limit is in Portugal at about 40°20'N.

2.2 Local vertical and horizontal distribution

The upper limit of L. hyperborea is usually just above LAT (lowest astronomical tide) (Kitching, 1941; Kain, 1962) or depressed below this under conditions of extreme exposure to wave action (Kain, 1971a), by reduced salinity (Sundene, 1953) or occasional other factors. The lower limit is much more variable and depends on local factors. Light is the most obvious of these and in very turbid water such as the Menai Straits off North Wales, the lower limit is only 2.5 m below LAT (Knight-Jones et al., 1957) and in some polluted areas the vertical range may be reduced to 1 m (Bellamy et al., in press). In clear water, however, the species can be found at more than 30 m below LAT, e.g. at 34 m in Norway (Kain, 1971a) and 36 m in southwest England (Whittick, 1969). Forster (1955) attributed variation on the Devon (southwest England) coast to turbidity, the lower limit near Dartmouth being 5 to 6 m and that off Stoke Point, in clearer water, 17 m. Another factor which can affect the lower limit is grazing (Jones and Kain, 1967).

Near the upper limit in exposed sites the plants are not normally the largest found in the area, presumably because of removal by wave action. The best developed forest is thus a few metres below the upper limit when the vertical range allows. With increasing depth the density decreases and the maximum size of the plants may get smaller. In some areas, e.g. the Isle of Man, the lower limit is determined by factors (such as grazing) acting on the establishment of the species rather than its later growth rate (Kain, 1963). In this case, the deepest plants are relatively large and grow only slightly more slowly than shallow plants. In other cases, e.g. in southwest Norway (Kain, 1971a), the deepest plants grow very slowly and are much smaller.

2.3 Effects of ecological determinants

This species is clearly unable to withstand prolonged exposure to the air. Its penetration into the intertidal zone is normally confined to considerably less than a vertical metre above LAT or to rock pools where it is totally immersed. Kitching (1941) attributes its lack of success in the intertidal compared with that of L. digitata to the greater exposure of the frond to desiccation, being held up by a stiff erect stipe. Lüning (unpublished) has observed mass mortality of L. hyperborea, with L. digitata surviving, after unusually low sea levels at Helgoland in winter. This may have been due to a lack of low temperature tolerance. The relatively inflexible stipe may also be more vulnerable to damage by breaking waves and cause more leverage on the holdfast than that of L. digitata.

L. hyperborea grows only on solid rock or stones or boulders large enough not to be turned over frequently by storms. On solid rock it grows on horizontal or upward facing sloping surfaces. It is rare on vertical faces or slight overhangs and then confined to small ledges. It is absent from completely downward facing surfaces. On large boulders with flat tops and steep sides the edges form a more favourable substratum than the central top under forest forming conditions because of less shading there by other plants. When normally stable boulders are turned over by unusually severe storms, plants of L. hyperborea with their stipes horizontal may survive for some time but the stipes bend to the vertical during growth.

There is no direct information on the temperature tolerance of mature plants of this species though there is some information on the

Fig. 4 The geographical distribution of L. hyperborea. The arrow indicates the uncertain Spitzbergen record.

early stages. It is likely that the optimum temperature (given adequate light) for gametophyte and young sporophyte development extends from 10° to 17°C (Kain, 1964, 1965). Above 17°C, the survival of gametophytes is progressively reduced, few surviving at 20°C, while sporophytes are produced up to 19° but not at 20°C (Kain, 1964, 1969). However, sporophytes can grow at 20°C in the laboratory (Kain, 1965). In Portugal, at the southern limit of the species, the winter surface sea temperature during sporing drops to about 14°C so presumably young stages could survive initially further south. However, in this region the maximum summer temperature, which has to be tolerated by later sporophytes and mature plants, is 19° to 20°C (U.S. Navy, Hydrographic Office, 1944). It thus seems likely that later stages have an upper temperature tolerance similar to the early stages. Less is known about the tolerance to low temperatures. Young sporophytes grow slightly more slowly at 5° than 10°C (Kain, 1969) and can thus presumably survive lower temperatures. The surface sea temperature on the open coast in north Norway drops to about 3°C in winter (Saelen, 1950). On the west coast of Spitzbergen in summer (July to September) the surface temperature records vary from 2° to 6°C (Helland-Hansen and Nansen, 1912; Nansen, 1915; Svendsen, 1959). It is not clear whether the northern limit of the species is determined by winter temperature or the lack of light during the obligate winter sporing season.

The quantitative light requirements of the early stages of L. hyperborea are known. Zoospores can undergo their first development in the dark and some can survive as early gametophytes in darkness for at least 80 days at 10°C (Kain, 1969). A minimum of about 2 µg. cal/cm^2 sec (or 20 lux of daylight) is necessary for the development of the gametophytes which are light saturated at about 60 µg. cal/cm^2 sec at 10°C but higher at 17°C (Kain, 1963). Very early sporophytes have light requirements similar to gametophytes (Kain, 1969) but both the compensation and saturation levels increase with increase in size. Below saturation the growth in light and dark periods is a product of the light period and the irradiance, e.g. 40 µg. cal/cm^2 sec for 12 hours in 24 would give the same growth rate as 20 µg. cal/cm^2 sec of continuous irradiance (Kain, 1964). The requirements of intermediate phases are not known but in mature plants the compensation point for photosynthesis is about 60 µg. cal/cm^2 sec and saturation is at 300-500 µg. cal/cm^2 sec (Lüning, 1971). The amount of light reaching the habitat depends on surface irradiance, transmittance through the water and shading. Measurements of underwater light in the Isle of Man (Kain, 1966, 1971b) have shown that in mid-winter the irradiance at the depth of the deepest normal lower limit of L. hyperborea at 15 m below LAT is probably of the same order as the minimum requirement of gametophytes and microscopic sporophytes. In the summer, however, these stages, but not later sporophytes, could well be saturated at this level. At shallower depths if there is no shading, all plants could be saturated in summer down to 5 m but almost all would be light limited in winter, though growth would be possible except where shading is severe. These estimates are supported by observations of growth at different times of year at these depths. In Helgoland (Lüning, 1971), even at 2.1 m below LAT the irradiance does not rise above the compensation point for fronds until April and only in June and July is it above saturation. This is attributed mainly to seston stirred up by storms in winter. It is likely that off the southwest coast of Norway (Kain, 1971a) light penetration through the sea is better in winter than off the Isle of Man. Irradiance levels in deeper water may thus be higher. In addition to transmittance through the water shading is a very important factor. Small algae, silt, etc. can cause severe shading on the rock surface and must reduce considerably the irradiance important for the growth of the very early stages, even in a fairly open community. The Laminaria forest itself, of course, is far from being open and also causes considerable reduction in irradiance. Kitching (1941) found that thick L. hyperborea forest in Scotland cut out 98.8 to 99.1 percent of the light. On the other hand, in preliminary measurements in the Isle of Man (Kain, unpublished) it was found that this species cut out only about 75 percent of the irradiance.

L. hyperborea thrives in moderate water movement. The stipe has enough flexibility to bend to and fro with the horizontal movement of wave action on the bottom subtidally. It cannot withstand severe breaking waves, however. Its place at the top of the subtidal zone is then taken by Alaria esculenta (Kain, 1971a). It thrives also in sites exposed to strong currents, for example at the entrances to sea lochs and fjords. Where there is little or no water movement the plants develop into f. cucullata.

Little is known of the salinity tolerance of the species. In an experiment on the early stages, Hopkin (unpublished) observed very occasional and slow sporophyte development following gametophyte maturation at 16‰S but not below this. It is almost certain that its absence from the Baltic is determined by the reduction in salinity. It occurs in the outer part of the Oslofjord only from 8 to 25 m, its absence from the shallow subtidal being attributed to reduced salinity (Sundene, 1953). Moving southward along the west coast of Sweden, the upper limit is progressively depressed (Michanek, private communication) to 15 m or deeper. The plants are much smaller than usual (Kylin, 1907; Levring, 1953). The salinity at the inner limit of the species is probably

between 25 and 30‰S (Levring, 1953; Michanek, private communication). In Loch Etive in Scotland, the inner limit of the species coincides with a salinity of about 26‰S (Powell, unpublished).

In the sites on the northeast coast of England studied by Bellamy et al. (in press) both the productivity and the depth range of L. hyperborea were found to be reduced in polluted sites. In sites with turbid but unpolluted water the depth range was reduced less but the productivity in shallow water was even lower. Reduction in productivity in both cases was attributed to decreased light penetration. The difference between the groups was attributed either to the more intermittent nature of the unpolluted turbidity, due to weather conditions, or to some relative stimulation of growth by nutrients in polluted water. The latter explanation seems unlikely if light is limiting growth. There is no evidence, in this area, of inhibition of the growth of this species by polluting substances other than through the reduction of light penetration. This is supported by experiments on the early stages (Hopkin and Kain, 1971) in which there was no inhibition by water from the River Tyne estuary provided that the salinity was adjusted. Further laboratory experiments (Hopkin and Kain, 1971) have shown that a number of household detergents are not toxic at a level likely to be found in the sea, though heavy metals and a herbicide could be. After severe oil pollution and subsequent detergent treatment on the southwest coast of England, no deleterious effect on populations of L. hyperborea could be detected (Bellamy et al., 1967).

2.4 Nutrition and growth

2.41 Assimilation

It is assumed, in view of the lack of evidence to the contrary, that L. hyperborea is autotrophic.

The photosynthetic rate shown by zoospores or early gametophytes for the first two days after release only just balances respiration even in saturating irradiance (Kain, 1964). The saturating irradiance for the growth of early stages (see 2.3) is low compared with most planktonic and many benthic algae so far studied. There have been no measurements of the rate of photosynthesis (in terms of carbon fixed per unit dry weight) of the early stages.

Lüning (1971) measured the gross photosynthesis of new and old fronds at different times of year in relation to irradiance. He found that the new frond was light saturated at about 400 µg. cal/cm^2 sec in March at 4°C, at about 500 µg. cal/cm^2 sec in May at 8°C and August at 16°C but at about 200 µg. cal/cm^2 sec in November at 10°C. The old frond (when a new one was present) was saturated at about 300 µg. cal/cm^2 sec in March and May. At the same time the light saturated gross photosynthetic rate increased in the new frond from about 1.8 ml O_2/dm^2 hour in March to around 3 ml O_2/dm^2 hour in May and August and was reduced to about 1.3 ml O_2/dm^2 hour by November. In the old frond the level was around 1.8 ml O_2/dm^2 hour in March and May. The increase in saturation level and gross photosynthesis in the summer were probably due to adaptation to increased irradiance in the habitat. Lüning (1971) also calculated net photosynthesis at 100 and 400 µg. cal/cm^2 sec at the same times of year. At the higher irradiance there was an increase in the new frond from March to May from about 1.5 to about 2.3 ml O_2/dm^2 hour and this remained the same until August and then dropped to about 1.2 ml O_2/dm^2 hour in November. In the old frond the figures for March and May were about 1.0 and 1.8 ml O_2/dm^2 hour respectively. Thus, although respiration increases with higher temperatures in the summer (see 2.42), the high irradiance and adaptation of the frond allows plenty of assimilatory surplus at this time of year. The lower figures for the old frond are attributed to ontogenetic change. At the lower irradiance, however, the summer respiration rates are relatively more important, so the net photosynthesis falls from about 0.5 ml O_2/dm^2 hour in March to about half this in May and August. Net photosynthesis of the old frond at the low irradiance is higher than the new frond because of lower respiration rates.

In a series of neat experiments, Lüning (1969b, 1970a) has demonstrated how growth of the new frond during the early months of the year can take place not only as a result of its own assimilation but using material from the old frond and stipe. He first showed (Lüning, 1969b) that the new fronds on plants on frames in the sea at 2.5 m developed the maximum area during the fast growing season only if both old frond and stipe were present. Plants with either of these amputated produced smaller new fronds. In whole plants kept in the dark the new fronds grew appreciably. He also found that amputation of most of the frond in September affected the size of the new frond produced. From these observations he concluded that growth of the new frond was partly at the expense of material from both the stipe and the old frond. This he took as an explanation for the observation that, in young plants at least, each annual frond is normally larger than the last (see 2.44). In later experiments (Lüning, 1970a) on variously amputated plants in complete darkness new fronds grew only slightly when isolated from old fronds, with or without the stipe. With the old frond present there was considerable growth, particularly without the stipe being present. Thus it seems that in darkness the stipe does not supply storage material to the new frond but may parasitize it, for the production of new stipe and haptera. Lüning suggested that about

30 percent of the new frond area produced during rapid growth is due to storage material in the old frond. Lüning (1971) also showed that the old frond could contribute to the new frond growth through its own assimilation. He exposed the old frond to labelled bicarbonate and light and found a gradation (from the collar downward) of activity in the new frond, which was isolated from contamination. In further experiments on translocation, Lüning et al. (in press) placed labelled bicarbonate in a small chamber glued to part of the illuminated frond. They found that transport took place almost exclusively basipetally and was confined to the large medullary elements in a longitudinal strip corresponding to the position of the chamber. When the latter was on the old frond this active strip narrowed at the collar and widened again in the new frond. Transport was still active 24 hours after exposure, but labelled material had mainly accumulated near the transition zone after 48 hours. The export of material outside the tissue exposed to labelled bicarbonate (which was part of the old frond when this was present) did not exceed 1.5 percent but was much higher in April, during the fastest growth of the new frond, than in January or October.

The general picture that emerges from these experiments is as follows. At the start of the fast growing season (see 3.31) in November or December, the irradiance in the habitat may well be below compensation (Lüning, 1971; Kain, 1971b) and growth takes place at the expense of storage material, mainly in the old frond. As light conditions improve both old and new frond assimilate and this material is incorporated into the new frond. The highest assimilatory surplus is in the summer months (Lüning, 1971) and allows a larger frond than in the previous year in young plants with stipes which are self-supporting in terms of assimilation. Lüning (1970a) suggests that, because old stipes are heavily infested with epiphytes and epizoans, assimilation may not be possible and these are parasitic on the fronds. This could explain why older plants do not produce successively larger fronds each year.

2.42 Respiration

Lüning (1971) measured respiration rates of fronds at different times of year. Taken on the basis of rate of oxygen production per unit of frond area, there was a slight increase from March to August. However, as the frond thickness changed during this time quite different results were obtained on the basis of dry weight. Then the value for the new frond increased from about 0.2 in March to about 0.7 ml O_2/g hour in May and dropped to about the March value in August and December. As storage materials increase during the summer Lüning also expressed these as volume of oxygen per unit weight of crude protein. The maximum was still in May, being 6.9 ml O_2/g protein hour respectively. The old frond did not show the high May rate, remaining at about 0.2 ml O_2/g dry weight hour. High respiration was thus associated with fast growth and not with temperature, suggesting adaptation to ambient sea temperature.

Experiments on cell-free preparations of L. hyperborea (Johnston and Davies, 1969) have indicated that many of the respiratory enzymes present in other plants and animals are present in this alga. The actual biochemical pathways could not yet be defined, however.

2.43 Nutrition

It is well known that species of Laminaria accumulate ions from sea water, some to quite high concentration factors, but there has been little work on L. hyperborea.

Little is known of the nutritional requirements of this species. It is normally assumed that nitrate and phosphate are necessary additions to sea water for laboratory experiments and there is little development of the early stages in stagnant sea water with no additions. Harries (1932) added small quantities of potassium nitrate and phosphate to L. hyperborea cultures every 10 days and investigated the effect of different iodine additions. She claimed that low concentrations of the latter had a stimulatory effect. There has been no further evidence that this species requires a higher concentration of iodine than is present in natural sea water. Growth of the early stages in the laboratory in Kain's (1964) medium of natural sea water enriched with 1.0 mM KNO_3, 0.1 mM K_2HPO_4, 0.005 mM $FeCl_3$ and eleven vitamins is as fast as has been recorded for Laminaria.

2.44 Growth

Under optimum conditions in the laboratory the gametophytes mature and produce gametes in about ten days from the release of zoospores. In the case of the female, this may not involve cell division but only differentiation and increase in size. The male, although smaller, always becomes multicellular. Under sub-optimal conditions maturation takes longer and there may be vegetative growth of the gametophytes prior to gamete formation.

The first two divisions of the zygote occur in quick succession but after this cell division of the sporophyte takes place about every 45 hours under optimum conditions and while the plant is still monostromatic. This results in a plant of 1 000 cells in 20 days from spore release (Kain, 1969). During this phase the growth has been shown to be two-dimensional with slight increase in cell size but very little change in plant shape (Kain, 1965). There is therefore a straight-line relationship between the logarithms of sporophyte length and cell number. The relationship is such that a

sporophyte of 1 000 cells would be about 1 mm long (Kain, 1969). This species has not been observed further in the laboratory but has been measured attached to slides in the sea (Kain, 1965). The plants were found to continue logarithmic growth in length at least up to 10 mm. The rate of growth in length was about 10 percent/day, half that observed under optimum conditions in the laboratory, but as the plant was by this time mainly polystromatic, this must have involved a similar rate of cell division. At this observed rate of growth, it would take a sporophyte of 1 mm 25 days to reach 10 mm. The total time from spore release would thus have been 45 days. This rate of growth may rarely be achieved in the sea.

There is less available information on the rate of growth from this stage onward. It is difficult to find the maximum rate of cleared areas in the sea because of competition from faster growing opportunists such as Saccorhiza and Desmarestia during the first year. Kain (unpublished) has observed growth on cleared areas on the submerged blocks of the ruined breakwater at Port Erin, Isle of Man. One block was cleared in November in such a way that only plants of less than 10 mm could have remained. From successive samplings from the block, the largest plant of L. hyperborea was measured. The growth in length was roughly logarithmic for about five months (after which competition was serious) and corresponded very approximately to 2 percent/day. As this was during the winter, although in shallow water (1.7 m below LAT), light was probably limiting so the potential growth rate must be faster. On another block cleared in August, one plant showed a rate of at least 3 percent/day during the first three months. Thus, at the fastest rate observed so far, it would take a plant 145 days from spore release to reach 200 mm. There is no doubt that this rate could be faster under optimum conditions, possibly including weeding out of competitors.

Further observations of these cleared blocks will be published at a later date. A few measurements can be mentioned now. Table I shows the stipe and frond lengths of the largest plant of L. hyperborea removed from a 0.5 x 0.5 m quadrat after the first, second and third year of growth on blocks cleared in November in three successive years. It also shows the lengths of the largest of 20 plants remaining on unsampled parts of these blocks and measured in situ. The growth rate after the first year was probably nearer to the maximum than during the first year because there was little competition from other species.

Lüning (1971) has followed the growth in frond area and stipe length of plants initially nearly two years old at a depth of 2.1 m below LAT for two and a half years. Figure 5, taken directly from his paper, shows this. Increase in a new frond area is apparent by February and there is a rapid increase in April and May which has ceased by July. During the slow growing season a considerable area is lost from the frond. The frond produced in each subsequent year is larger than the previous one. When Lüning (1970a) grew second year plants on frames at different depths, he found that the maximum frond area was reached in June at 2 m and not until July at 6 m. The July frond area was the same at each depth but the stipes at 6 m were only a third of the length of those at 2 m. The frond: stipe ratio was therefore higher deeper. The situation was similar in third year plants.

John (1968) grew transplated "first year" (at the start) plants of L. hyperborea on frames suspended in the sea at 1.3, 7.4 and 13.5 m below LAT for a period of five months covering most of

TABLE I

Stipe length + frond length in mm of largest plant in sample from cleared blocks at 2 m below LAT at Port Erin, Isle of Man

Block cleared in November:	1 year	2 years	3 years
1967	270 + 400	340 + 760	740 + 860
1968	90 + 350	340 + 800	
1969	100 + 410		
Longest stipe length of plants measured in situ:			
	280	580	740

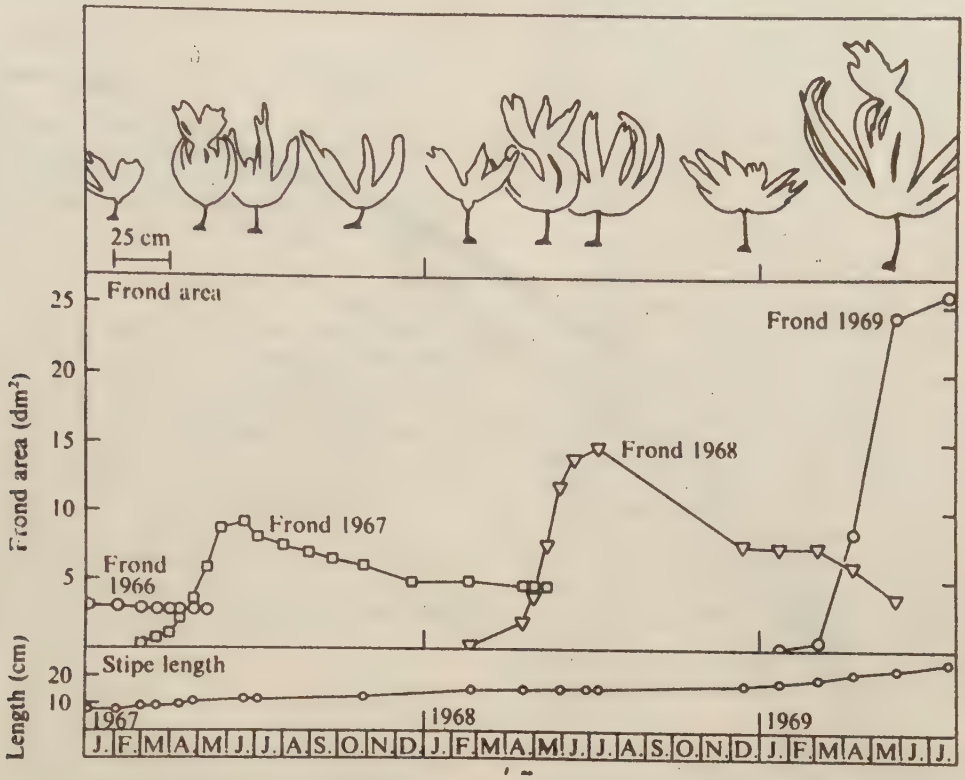


Fig. 5 Records of the growth of frond and stipe of L. hyperborea at 2 m below LAT in Helgoland (from Lüning, 1971).

the fast growing period. As the old fronds were cut off before the experiment, growth may not have been maximal. At 1.3 m the stipe length about doubled, at 7.4 m it increased by about half and at 13.5 m there was almost no stipe growth. The frond, however, grew at all depths, at 1.3 m to nearly 10 times its original length, at 7.4 m to about five times and at 13.5 m to about 2.5 times. These figures are very approximate because of individual variation but the differences between the depths are clear. The results agree with Lüning's in that there is more reduction in stipe than frond growth with increasing depth.

Growth of the frond of this species can be followed by observation of holes punched in it at various distances from the transition zone, as has been done in other members of the Laminariales (Parke, 1948; Sundene, 1964; Norton and Burrows, 1969).

The past growth of plants of a population can be assessed at any one time by measurement of the stipe and frond weights and ageing of the stipe base (see 1.32). This method has been used by Bellamy et al. (in press) in terms of dry weight and by Kain (1971a) in terms of fresh weight. An increment is calculated for each year of life, remembering that the stipe is perennial and the frond annual. Thus the stipe increment is taken as the difference between the mean stipe weight of an age group and that of the previous age group and the frond increment as the mean frond weight for that age group. The results for each successive age group are then added together. The population should, of course, be sampled at the end of the fast growing season when fresh weight is used but later for dry weight. Some cumulative fresh weights for various populations calculated by this method are shown in Figure 6. The disadvantages of the method are first that the error, too, is cumulative and second that any one year may not be representative.

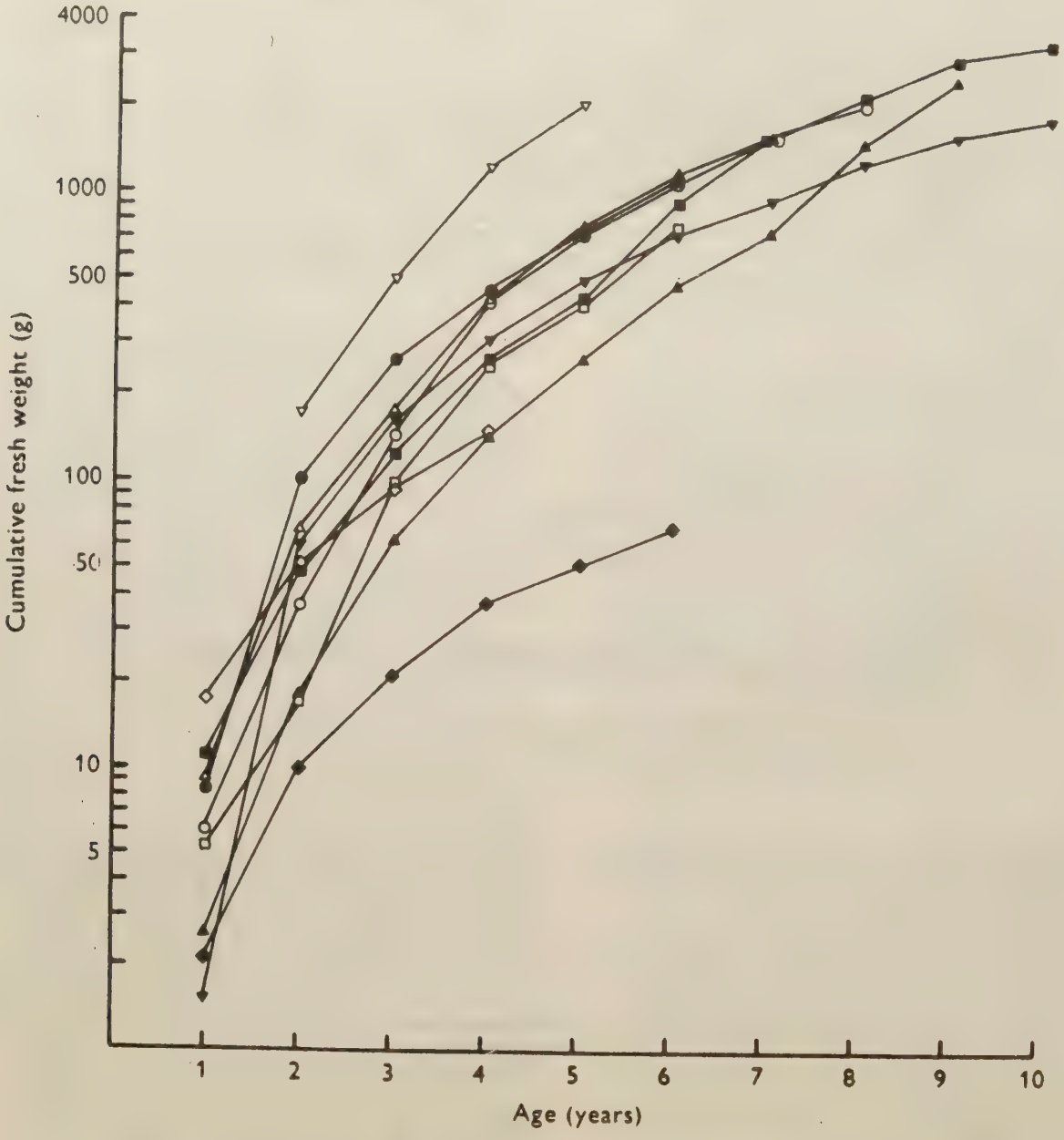


Fig. 6 Cumulative fresh weight production in populations in the Isle of Man and the Espegrend area (see Tables IX and II for positions and depths).

○, MS4
△, ME4
□, ME14
◇, ME22
●, BS4
▲, BE4
■, BH14
◆, BE33
▽, BCu0.5
▼, BS18

(From Kain, 1971a)

3 LIFE HISTORY

3.1 Life cycle

3.11 Alternation of generations

L. hyperborea shows marked heteromorphic alternation of generations typical of the order. The large habitat dominating sporophyte alternates with microscopic dioecious gametophytes which have not yet been observed in the field.

3.12 Nuclear phases

Evans (1965) showed that the gametophytes were haploid with about 31 chromosomes and young sporophytes, providing there had been fertilization, diploid with about 62 chromosomes. Schreiber (1930), after separating gametophytes, showed that unfertilized eggs could develop into parthenogenetic sporophytes which survive for a limited period. This has been confirmed (Svendsen and Kain, 1971). Evans (1965) had one count of 36 chromosomes in a young sporophyte of this species. This could represent the haploid number and be explained by parthenogenetic development of that sporophyte.

3.2 Reproduction

The zoospore is about 5 µ in diameter (Sauvageau, 1918), and is pear shaped with two lateral flagella and a curved chromatophore (Williams, 1921). Sauvageau (1918) found no eyespot though he did find one in Saccorhiza. Kanda (1936, 1944) found none in several species of Laminaria. However, Kuckuck (1912) showed an eyespot in L. saccharina zoospores. As Saccorhiza zoospores are phototactic and those of north European species of Laminaria are not (Kain, 1969), it seems likely that Sauvageau was right.

Liberated zoospores can remain motile for up to a day in the laboratory and when motility is lost they round off, form a cell wall and may remain planktonic for some days, slowly sinking (Kain, 1964). They are fairly sticky and adhere to surfaces. After rounding off, the cell extrudes a germination tube (Fig. 7) into which most of the cytoplasm and the chromatophore, divided into two, pass (Williams, 1921). The tube swells at the end to at least the size of the original spore, the nucleus divides and one passes into the enlargement with most of the cytoplasm and chromatophores and a wall forms across the tube (Williams, 1921). The nucleus and cytoplasm remaining in the original spore degenerate. This is called the dumb-bell stage and it can be achieved in the dark and while still planktonic.

From this stage onward the development of the male and the female gametophyte differs. In the male the enlargement swells but soon divides into several small cells in a cluster (Fig. 7, left). These divide further and under optimum conditions in the laboratory there are at least five pale cells by the time the gametophyte is mature, within 10 days from spore liberation (Fig. 7, left). Any cell can become an antheridium, the apex of which swells and forms a cap, bursts and releases a single antherozoid from the gametangium (Williams, 1921). Schreiber (1930) found that male survival was favoured over female in prolonged cultures, perhaps affected by increasing salinity with evaporation.

For a while the effective cell of the female gametophyte merely swells spherically. It may then divide but under optimum conditions usually does not. It then elongates, to the shape shown in Figure 7 (right). The tip of the process thickens and chromatophores crowd into it (Williams, 1921). A slit then appears in the tip and the contents of the oogonium pass out through the gaping opening. The egg is spherical and about 12 µ in diameter. The end wall of the now empty oogonium closes and forms a cup-shaped platform on which the egg may rest. Williams (1921) was the first to confirm fertilization though he did not actually see it. He saw eggs surrounded by active antherozoids and nuclei in various phases of fusion. After fertilization by a male gamete a wall forms round the zygote. The continued development of the sporophyte is shown in Figure 8.

Although zygotes are formed within 10 days in the laboratory under optimum conditions, gametophytes can develop quite differently under other conditions. Schreiber (1930) maintained his cultures in sea water with only nitrate and phosphate added in an unheated room in reduced daylight. His cultures were unialgal and devoid of protozoa; this he achieved by careful washing of individual early gametophytes. His gametophytes developed extensively vegetatively, each one eventually becoming a tangled mass of filaments (broader in the female than the male) several millimetres across and thus macroscopic. Kain (1964) found that similar filamentous gametophytes developed in unchanged medium providing that the irradiance was low. Figure 9 shows these at an early stage in development. In saturating irradiance the gametophytes become mature before whatever factor that may cause filamentous development in unchanged medium becomes effective. Filamentous gametophytes of Schreiber's type have been maintained for a few years in low light at 10°C (Svendsen and Kain, 1971). The conditions causing this vegetative growth have yet to be defined.

Filamentous gametophytes may be entirely vegetative, may have occasional gametangia or under the right conditions may produce many gametangia. There is thus a far greater potential in terms of gametes in this type of gametophyte. Under optimum laboratory conditions a female produces only one egg and then dies, while filamentous gametophytes can produce thousands over a period of years. The latter can also be

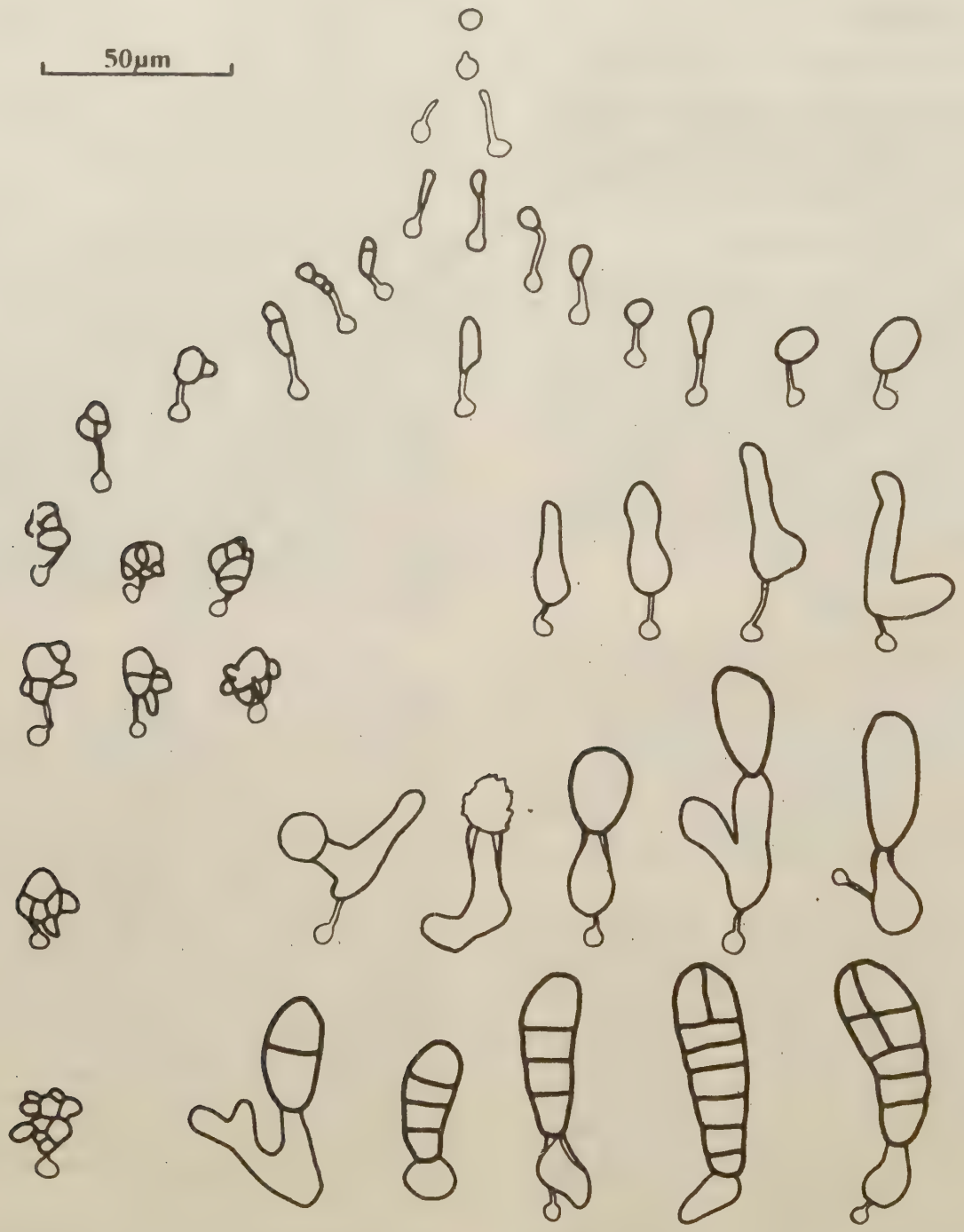


Fig. 7 Drawings from culture under optimum conditions of development from zoospores (top) of male (left) and female (right) gametophytes to maturity, the production of a zygote (third row) and its initial development as a sporophyte (fourth row).

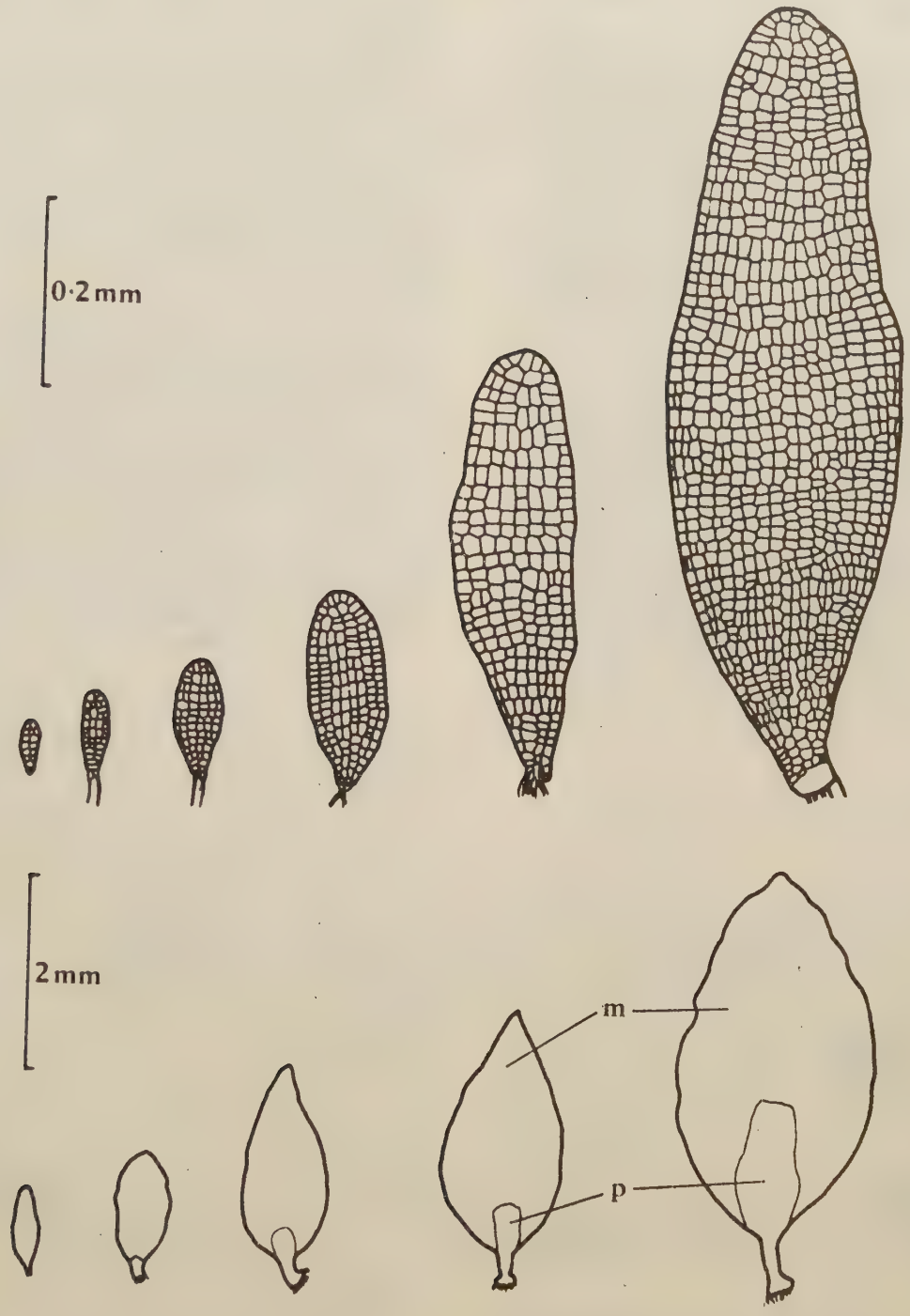


Fig. 8 Drawings of developing sporophytes. Top row from Sauvageau (1918).

m = monostromatic p = polystromatic

fragmented and the various parts continue growth and reproduction.

The factors determining gamete formation in filamentous gametophytes remain obscure. In several experiments Schreiber (1930) found that gametes were formed in winter or in artificially induced low temperatures of 2 to 4°C but were sterile at higher summer temperatures. However, in saturating irradiance, gametes are freely formed at 18°C (Kain, 1969) and filamentous gametophytes become rapidly fertile at 10°C in new medium in saturating irradiance (Svendsen and Kain, 1971). Thus, there seems to be an interaction of factors determining the onset of fertility in L. hyperborea gametophytes.

It is not known what type of gametophyte exists in the field and how in situ conditions affect the morphology. Sterlized stones left at 2 m below LAT on Port Erin breakwater for two months at different times of year and then examined under a microscope bore L. hyperborea sporelings only during the sporing season, as might be expected (Kain, unpublished). On the adjacent block, however, which was scraped every two months, sporelings of this species arose all through the year. This suggests that gametophytes might have been present all the time but the explanation might also be that minute sporophytes were lying dormant until able to grow in increased irradiance (due to the clearing).

The spherical zygote is considerably denser than sea water and if it is not stuck to the oogonium neck it could fall away from a very steep or overhanging surface. This may be why the species is absent from overhangs, though the behaviour of the zoospores could be responsible. If the zygote is in the proximity of the oogonium in culture when it produces its first rhizoid this usually attaches on to the neck (Sauvageau, 1918).

The development of the sporophyte from the zygote has been followed in the early stages by Sauvageau (1918) and others. The zygote elongates and the cross wall divides it into an apical and a basal cell (Fig. 7, bottom row). The next division can be in either direction, resulting in four cells in a row or in a cruciate form. For some time cell divisions tend to be simultaneous so that many groups of four or 16 cells can be seen to be aggregated (Fig. 8). At this stage the plant remains monostromatic. At approximately the 30-cell stage a rhizoid is formed from a basal cell and more develop later. The shape of the plant is roughly elliptical

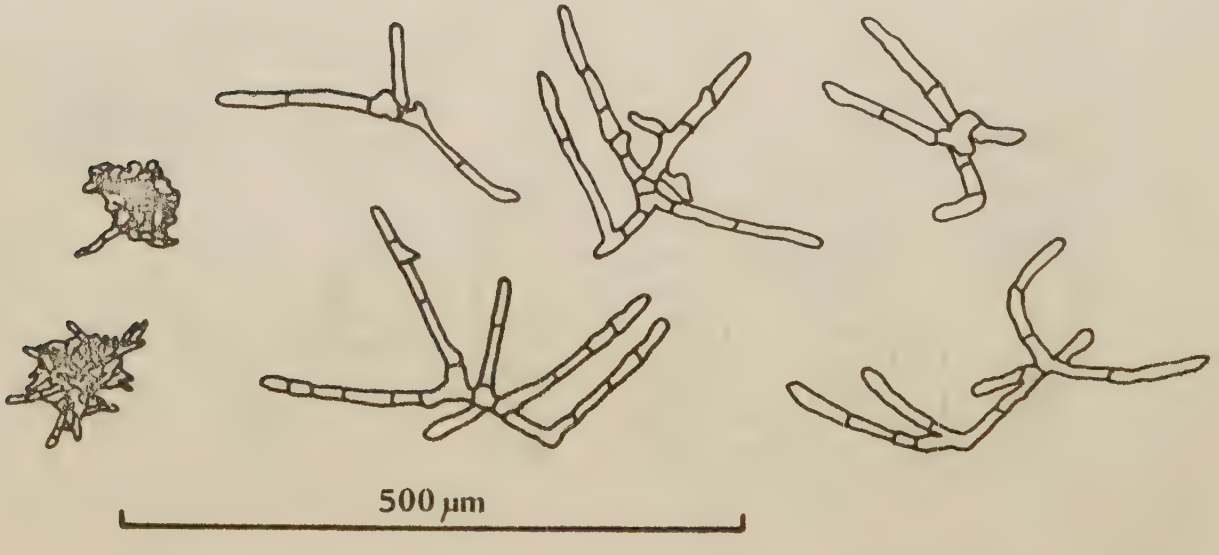


Fig. 9 Drawings of filamentous male (left) and female (centre and right) gametophytes grown in culture in suboptimal light without change of medium.

(Fig. 8). As development proceeds, there is periclinal as well as anticlinal division at the base of the plant, resulting in a polystromatic region which will become the stipe. Gradually the base of the frond also becomes polystromatic (Fig. 9 p) and the stipe terete. At some stage (at about two months in L. digitata according to Killian, 1911) growth becomes localized mainly in the transition zone though also in the surface layers as more of the frond becomes polystromatic, being two, three and four layered and leaving only a tip of the original monostromatic tissue. A disc is formed at the base of the stipe and this is fixed to the substratum by rhizoids on its lower surface. Eventually medulla cells are formed from cortical cells in the stipe and frond in the way already described (see 1.32). Later, the first whorl of small haptera grow out above the disc and form further attachment.

Whether or not growth slows during the first slow growing season depends on when a young sporophyte arose and probably on conditions.

It can be seen from the developmental stages in the figures that the frond:stipe ratio is high in very young sporophytes, even before the shedding of the first frond.

In normal growth the sporophyte of L. hyperborea obligatorily has only one holdfast, stipe and frond. New stipes cannot arise from the holdfast as they can in some species in the genus. There is thus no vegetative reproduction of this phase. The region of paramount importance is the transition zone. If this gets damaged in a particular way, a freak frond can develop, and if it is split longitudinally into two without too much other damage, the divided stipe and frond can continue growth in two parts. If the zone is cut transversely, losing the frond, the stipe can continue growth for a short while only (Kain, unpublished), during the growing season. If the transition zone is destroyed, then the plant is incapable of further growth and dies.

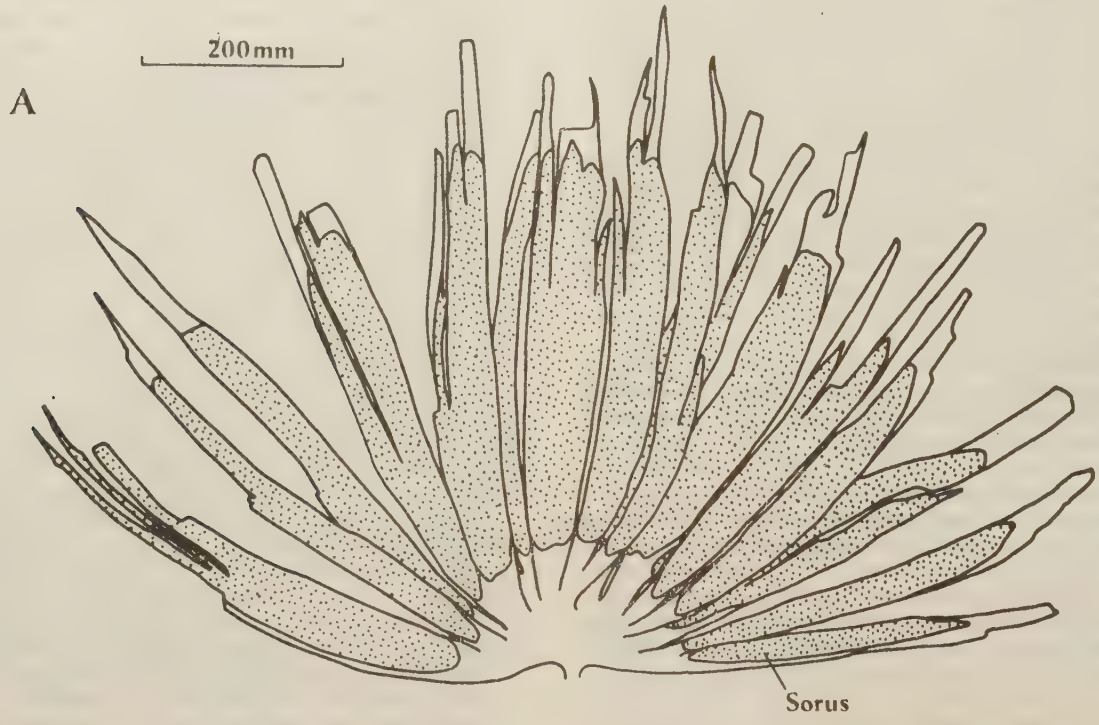
The earliest age at which a sporophyte of L. hyperborea has been observed to become fertile is about 15 months (Kain, unpublished) but this is unusual. Some have been observed at 18 months and almost all plants on cleared areas at 2 m below LAT which were two years old near the beginning of the sporing season have been observed to spore. However, the maturity of the sporophyte probably depends on size as well as age, so in a forest where growth is slower than on cleared areas, fertility may well be arrived at later. This is supported by the observation that two-year olds on cleared areas in deeper water (6 m), where growth is slower, did not become fertile during the sporing season. Of 100 marked plants in virgin forest only 75 percent of the four and five-year olds spored while all those of six and over did (Kain, unpublished).

The sporing season has been recorded in the Isle of Man by Kain (unpublished). The earliest fertile fronds appear in the middle of September and the latest disappear near the middle of April. Between these dates there is a steady increase to about 40 percent of mature plants sporing at the beginning of January and then a steady decline. Labelled plants observed at intervals spored for a mean of 6.5 weeks each but there was considerable variation in the duration. Out of 160 only four plants spored over two separate periods and in each case the second sorus to appear was small and on part of the frond that had not previously borne sporangia. Parke (unpublished) recorded the sporing of labelled plants near low water in Devon, southwest England and found a later and more intense peak to the sporing season in February. Rees (1928) also recorded a later season, of February to May with a peak at the end of March, in Wales. The Isle of Man observations have been made over a period of 12 years and differ only slightly from year to year so the differences between these sets of observations must be due to the locality or, more likely, to the selection of populations in Devon and Wales. Even in the Isle of Man it has been observed that a group of plants of very similar age may show a closer timing in their fertile periods than the general population, and the peak may be in a different month. It appears that near the north of its range too this species produces spores in winter (Kain, 1971a).

Nothing is known of the time of day of spore emission.

Sori develop only on the old frond and in mature plants cover all but the distal and proximal parts (Fig. 10A). The sorus on each finger of a digitate frond extends to about 2 mm from the lateral edge but there may be 50 mm or more of sterile frond at the tip. Near the transition zone, or after the growth of the new frond, the collar between the fronds, there is an arc of sterile tissue. There is a sorus on each surface of the frond and these are normally exactly opposite each other. The coverage of mature frond surfaces devoid of epiphytes is 73 percent (Kain, unpublished). In young fronds sporing for the first time, the sori are smaller in relation to the frond and there is more of a gap on the proximal part. It is here that a second fertile area occasionally appears after the first sori have disappeared.

Certain epizoids and epiphytes affect the development of fertile tissue. Sori have been observed extending only up to about 2 mm from the active edge of Membranipora. The other side of the frond can apparently be affected by active growth of this bryozoan. Sorus formation can also be inhibited by small epiphytes. However, epiphytes can be found growing on the surface of a mature sorus (Jaasund, 1965).



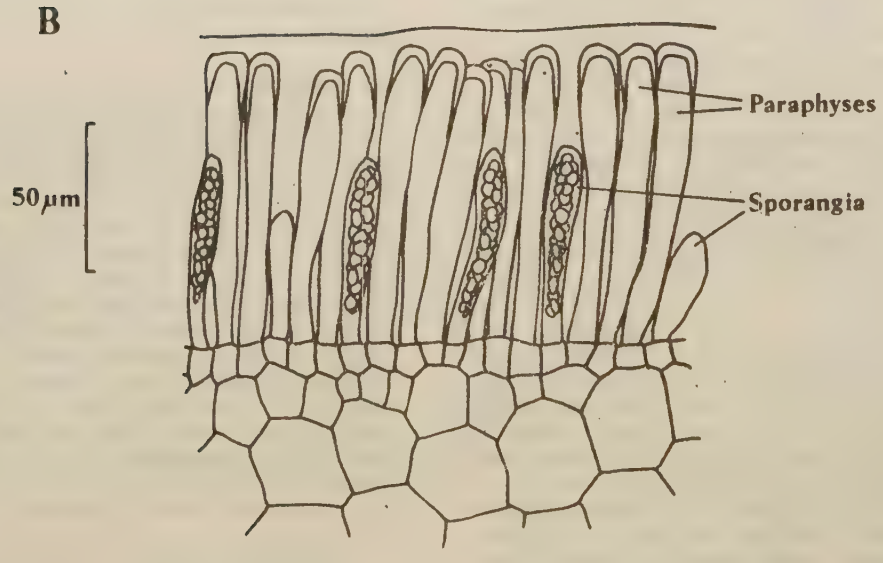


Fig. 10 The sorus in L. hyperborea

A. Drawing of fertile frond. Stippled area: sori on both surfaces.

B. Transverse section of sorus showing unilocular sporangia and paraphyses.

The sorus, which develops from the superficial cells of the frond, is a mixture of club shaped paraphyses and unilocular sporangia (Fig. 10B). The paraphyses have gelatinous thickenings at their distal ends which adhere together and form a tough covering to the sporangia. The latter are shorter, oval shaped and can usually be seen in various stages of development. Whether there are progressive crops of these, as claimed for L. saccharina (Parke, 1948) is not known. There are about 7 300 sporangia (including developing ones) per square millimetre of frond surface area. Schreiber (1930) found that of the 32 zoospores produced in each sporangium, half were potential male and half potential female gametophytes. Thus sex is genotypically determined. Schreiber described sporangial dehiscence. The contents, surrounded by a membrane, exit with a jerk from the sporangium and move slowly outward through the paraphyses, probably pushed by their pressure, leaving the empty sporangium still attached. The ball of zoospores remains intact outside the paraphyses for some seconds and then an opening appears and the zoospores swim out.

3.3 Phenology

3.31 Seasonal variation in external appearance and morphology

Because L. hyperborea is a perennial plant the seasonal changes are mainly in individual morphology rather than in population numbers. These changes are associated with the marked variation in growth rate with season. The fast growing season starts in November when the transition zone becomes paler and a flattened swelling appears at the base of the frond. The onset is remarkably sudden, all plants starting within weeks of each other. This swelling, which is the new frond, gradually expands into roughly the shape of a thin disc, merging with the stipe below and the old frond above. When the connexion with the old frond is narrower than the new frond the zone between them can be called the collar. Its presence is characteristic of the species grown under widely differing conditions. The new frond expands further (Fig. 1B) and becomes progressively thinner. It remains paler than the old frond. By March, under turbulent conditions, longitudinal splits have appeared in the frond and the outer fingers may have been freed from the collar (Fig. 1B). By April the new frond approaches the size of the old. By July growth has ceased. This sequence of events takes place somewhat later in deeper water than in shallow (Lüning, 1970a). The time of separation of the old frond from the new depends on water movement. It thus depends on the degree of shelter of the coastline, the depth and the incidence of storms. It can thus vary considerably from year to year at one site. Under turbulent conditions the old frond can be lost in early March while very sheltered old fronds of f. cucullata can be retained until October (Svendsen and Kain, 1971). However, most of the old fronds are usually lost in March to May; at any one site those in shallow water go before the deeper ones (Lüning, 1970a). The arrival on the beach of a mass of fronds is often called the "May cast".

Concurrently with frond growth, the stipe elongates through addition to its distal end by the transition zone. The new stipe is pale and smooth, it being some months before the papillae on its surface appear and these too are paler than the old ones. The new part of the stipe is devoid of epiphytes for some time.

The new growth of haptera, in a ring above the last, is more variable in its timing. The first knobs may appear in January and the haptera reach the bottom by March, or they may not appear until July. The earlier appearance may be confined to younger plants and some older plants do not produce haptera every year.

After the shedding of the old frond, the plant is usually fairly free of epiphytes and epizoids from the transition zone upward for a while. The Laminaria forest in June and July thus has a relatively "clean" appearance, with most of the smooth brown fronds uncluttered by other organisms apart from Patina pellucida. The highly mucilaginous smooth surface is not a very hospitable substratum for most organisms. Frequently, however, many of the fronds are later colonized by the bryozoan Membranipora membranacea and it is clear that the surface of this is much more favourable for the settlement of epiphytes. By the end of the summer, particularly in shallow water, many of the fronds bear a considerable flora. During the winter, of course, most of the fronds bear sori, some before the new growth starts below them and some after. There may be further colonization by epiphytes, particularly on the parts that had been fertile before the frond is lost.

3.32 Seasonal variation in total fresh and dry weight

The total fresh weight of any mature plant varies considerably with the season because of the annual development of the frond. The maximum may be obtained sometime during the spring, just before the loss of the old frond or may be in July when the new frond is fully grown. The minimum may be in November, after some losses to the frond by tearing or grazing and just before the growth of the new one or in the spring just after the loss of the old frond. Maximum dry weight in Britain is from September to November (Whittick, 1969) when the frond contains a full complement of storage material. Whittick found that the dry weight of intact fronds in deep water fell faster in the winter than those in shallow water, presumably because of greater use of reserve material (see 2.41). Mechanical loss of fronds, however, must be faster in shallow water.

4 POPULATION

4.1 Structure

4.11 Age composition

The age composition of a population obviously depends on the history of the population and the environmental factors. Types of population can be broadly grouped in this respect. Figure 11 shows the age structure of some of the populations studied by Kain (1963 and unpublished). In the top line are populations from shallow water exposed to considerable wave action. They all show a predominance of young plants, presumably made possible by the continual removal of larger plants by wave action. The similarity of F2, collected samples from different sites in the Isle of Man at 2 m below LAT made in 1959, and ME4, collected from a single site at 1 m in 1966, encourages a generalization of this sort. In the second line are more sheltered shallow water populations. Here one would expect that without regular removal of large plants, more intermittent factors might allow the development of younger plants. Thus various ages dominate. In the third line are deeper populations where conditions allow thick forests to form. This is the most stable situation because storm damage is minimized and a broad age range made possible. This is shown well in SE10 and in BH14 but not in F5. The last was perhaps shallow enough for the mortality to be affected by wave action. Finally, in the bottom line, are populations from the edge of the forest, not much affected by the canopy, where the critical factor is one affecting the establishment of the species on the rock. Here intermittent factors are all-important and establishment is severely affected by the conditions in a particular year. In both 1962 (L2 and L10) and 1966 (ME14) there seemed to have been a good establishment year four years previously.

4.12 Weight or size composition

The method of aging plants of L. hyperborea instigated by Parke (unpublished) allows a determination of the size/age relationship within populations. For some time it was thought (Kain, 1963) that the stipe, being perennial, is a good measure of the growth of the plant throughout its life. However, it was later found (Kain, 1971a) that environmental factors can have a marked effect on the frond:stipe ratio so interpretations must be made with care when certain conditions differ. Table II shows the mean stipe fresh weights (with haptera removed) with fiducial limits ($p = 0.05$) for different ages in widely differing populations, taken from Kain (1963, 1967 and unpublished). Similarly Table III shows the frond fresh weights. Some of the data published in 1967 involved an overestimate of the plant age (Kain, 1971a). In only two populations, MCa4 and BE33, were the stipes all significantly smaller than in other populations. In both this may have been because of reduced light, the former being at 1 m below LAT but at the inner limit of the species in a cave, and the latter being at 33 m near the depth limit. However, in the former case, the type of water movement at this site, which caused damage to the meristem, may have been responsible for the small size. Small plants in deep water have been reported by Printz (1926) in Trondheimfjord. The stipe and frond weights of the plants in the Isle of Man sites from 1 to 6 m below LAT do not differ greatly. Differences in one-year olds may only reflect temporary conditions or the time of arising of most of the group and as size distribution is unlikely to be normal, fiducial limits cannot be relied upon. The lower stipe weight of the slightly more sheltered MS4, compared with ME4, may possibly be explained by the frond: stipe ratio being increased in sheltered water. This is shown much more clearly in BS4 (L. hyperborea f. cucullata) in which the stipes were very much smaller and the fronds larger than other populations. The fact that down to 20 m or so in these populations there is little reduction in stipe and frond weight is probably explained by the interaction of density and depth (see 4.22). The largest plants for their age in these populations were those of BCu0.5, in a fast current near Bergen. It is likely that by some accident the site had been cleared of vegetation some years previously, because the plants were all young, and that the environment was favourable for fast growth. Recent observations (Kain, unpublished) on cleared areas have indicated much faster growth rates than in established forests.

Tables IV and V show dry weights found by Whittick (1969) of stipes and fronds respectively, using the same method of aging as Kain, at four sites in Britain. It is clear from Tables II to V that there is more variation in size within an area and thus with local conditions than there is between the widely differing latitudes observed.

This is also apparent from Grenager's (1953, 1954, 1955, 1956, 1964) data. His measurements were all on plants of L. hyperborea which were brought up whole by the spring grab he used for surveys of quite large areas in Norway. The surveys were made after the end of the fast growing season. The plants came from a wide range of depths and sites in each case, so each set of observations is more collective than those by Kain. He counted the number of "rings" in the stipe. This is not quite as reliable an estimate of age as a longitudinal section but may often give the same result. His data for the mean total fresh weight and total length in plants with different number of rings in a number of areas

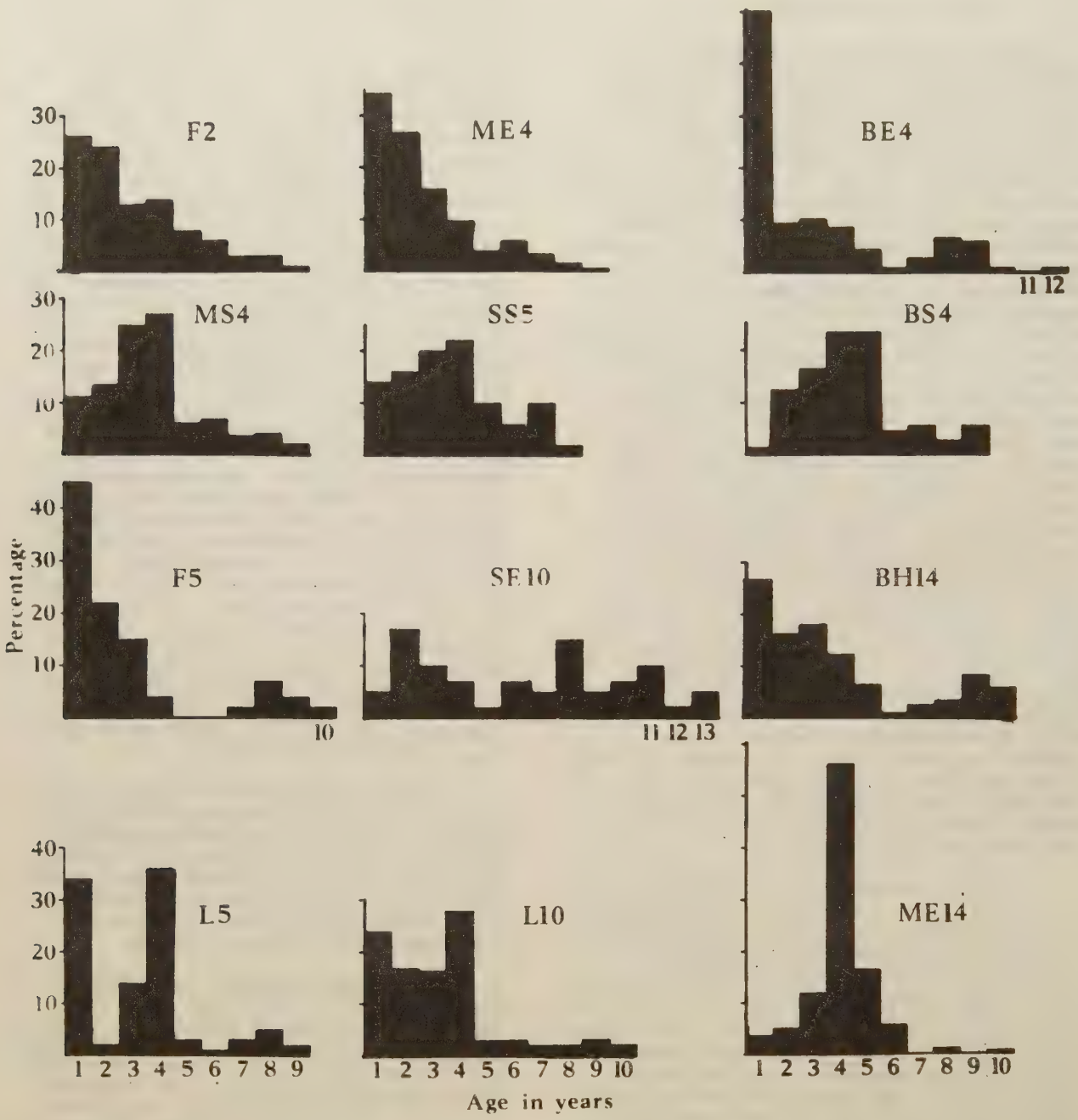


Fig. 11 Age structure of populations. Percentages of plants within age-groups. See Tables IX and II for site positions and depths. (From Kain, unpublished.)

TABLE II

Mean fresh weights of stipes at various ages in different populations sampled by Kain (1963, 1971a and unpublished). Fiducial limits at 0.05 shown in brackets. For latitudes and longitudes see Table IX.

Site	Depth m below LAT	Minimum age in years								
		1	2	3	4	5	6	7	8	9
MCa4	1	0.697 (±0.383)	5.32 (±2.07)	6.47 (±2.43)	7.68 (±2.99)	6.44 (±1.67)	14.7 (±10.4)			
ME4	1	1.89 (±0.75)	17.4 (±6.70)	45.3 (±10.8)	125 (±57)	236 (±112)	355 (±65)	424 (±57)		
MS4	1	0.906 (±0.467)	7.34 (±2.60)	45.8 (±12.1)	119 (±14)	132 (±25)	224 (±45)	298 (±24)	313 (±51)	348 (±37)
F2	2	22.0 (±12.2)	52.2 (±14.7)	136 (±48)	211 (±61)	425 (±75)	521 (±56)	553 (±76)	544 (±81)	
F5	5	9.62 (±3.67)	30.9 (±11.6)	61.0 (±18.0)		227 (±104)			722 (±203)	
L5	5	26.9 (±5.8)		78.8 (±25.4)	223 (±67)	313 (±46)	319 (±67)	378 (±60)	419 (±110)	
L10	10	21.2 (±4.5)	35.7 (±5.4)			143 (±57)				
ME14	11	0.604 (±0.426)	2.41 (±0.83)	27.8 (±12.3)	79.3 (±9.8)	110 (±27)	208 (±57)			
ME22	19	2.61 (±0.93)	7.42 (±3.71)	13.8 (±8.5)						
SS5	3		33.8 (±11.0)	46.9 (±13.3)	86.6 (±17.2)			225 (±69)		
SE6	3			181 (±53)	263 (±53)	247 (±116)				
SE16	14				120 (±52)					
BCu0.5	0		38.7 (±12.5)	92.3 (±32.7)	192 (±54)					
BE4	3.5	0.290 (±0.091)	3.60 (±1.57)						529 (±153)	733 (±105)
BS4	3.5	4.91 (±3.89)			24.2 (±6.4)	32.3 (±7.7)	61.7 (±36.1)			71 (±63)
BH14	14	0.821 (±1.44)	5.10 (±1.58)	27.9 (±13.5)	73.3 (±23.6)	115 (±50)			760 (±247)	949 (±91)
BS18	18					30 (±13)			61.4 (±18.4)	87.1 (±44.2)
BE33	33					4.46 (±2.62)	4.56 (±3.87)			
TE2	1	4.61 (±3.22)	18.2 (±6.2)							

TABLE III

Mean fresh weights of fronds at various ages in different populations sampled by Kain (1971 and unpublished). Fiducial limits at 0.05 shown in brackets. For latitudes and longitudes see Table IX

Site	Depth m below LAT	Minimum age in years								
		1	2	3	4	5	6	7	8	9
ME4	1	7.23 (±2.39)	43.9 (±15.1)	81.8 (±28.1)	181 (±74)	221 (±83)	288 (±76)	320 (±132)		
MS4	1	5.09 (±2.31)	25.5 (±7.3)	67.3 (±34.2)	203 (±40)	287 (±121)	277 (±90)		421 (±159)	
ME14	11	4.74 (±2.17)	10.3 (±5.1)	55.2 (±21.5)	108 (±15)	120 (±42)	258 (±111)			
ME22	19	15.1 (±5.0)	29.3 (±10.9)	37.4 (±19.6)	45.9 (±13.4)					
BCu0.5	0		132 (±62)	279 (±144)	616 (±187)					
BE4	3.5	2.32 (±0.55)	12.0 (±6.8)		54.6 (±31.8)			133 (±94)	546 (±244)	796 (±194)
BS4	3.5	87.7 (±64.2)	159 (±57.1)	182 (±61)	288 (±97)					
BH14	14	10.4 (±2.8)	33.4 (±10.2)	54.1 (±15.2)	92.0 (±22.3)	119 (±32)			431 (±84)	605 (±54)
BS18	18					182 (±80)			344 (±156)	274 (±108)
BE33	33				14.2 (±8.8)	14.8 (±9.8)				
TE2	1	16.7 (±11.8)	99.0 (±58.5)							

are shown replotted in Figure 12. It seems that the fresh weight approximates to a straight line rather than the more usual sigmoid curve for plant size against age. This may be due to the mixed nature of the samples. Plants in deep water grow more slowly and may not live as long as those at an optimum depth. Their mean fresh weight will thus reduce the mean for plants of medium age but not the older, largest ones. A similar effect may be produced by a dense canopy. Although Grenager's surveys extended from south Norway to near the northeastern limit on the mainland, there seemed no trend with latitude of either total length or fresh weight, at given age.

Black et al. (1959) collected a sample of 112 plants of L. hyperborea from about 24 km SSW of Oban, western Scotland, measured the stipes and observed rings. The mean stipe lengths with 7 to 10 rings ranged from 174 to 192 cm, whereas the mean stipe lengths with 7 to 10 rings in five of Grenager's surveys ranged from 78 to 150 cm. This difference could have been due to the Scottish sample being from a small (favourable) depth range, to particularly favourable conditions at the site, to a difference in the method of counting rings or to the relatively small sample size.

The maximum length attained varies to some extent with latitude. Sauvageau (1918) stated that maximum stipe length in France was usually about 1 m and the frond length rarely exceeded 1 m. This is true also of the Isle of Man; few stipes have been found measuring more than 1 m (Kain, 1963, 1971). However, in Scotland stipes of up to 2 m (Kain, unpublished) or even 3 m (Parke, unpublished) have been recorded. Grenager measured plants from his sampling sites (see Table IX) and the longest stipe lengths, with whole plant length in brackets, were as follows: Kvitsøy, 1.35 m (2.0); Karmøy, 2.2 m (3.1); Tustna, 2.5 m (3.0); Nord-Frøya, 2.0 m (3.2); S. Helgoland, 2.3 m (3.3); Helgøy, 1.3 m (2.1); E. Finmark, 1.5 m (2.4).

TABLE IV

Dry weights of stipes at various ages in different populations sampled by Whittick (1969). For latitudes and longitudes see Table IX.

Site	Depth m below LAT	Age in years								
		1	2	3	4	5	6	7	8	9
Sennen Cove	2			8.5 (±4.3)	22 (±6)	45 (±6)	46 (±4)			
	6		2.4 (±1.2)	11 (±3)	19 (±4)	38 (±2)	51 (±3)	76 (±14)		
	9		3.1 (±1.4)	12 (±2)	22 (±2)	32 (±10)	39 (±14)	45 (±13)		
	12				17.4 (±5.8)	29 (±3)	33 (±7)	34 (±6)		
Dunmanus Bay	1	0.51 (±0.18)	0.87 (±0.68)	4 (±2)	20.8 (±11.8)	42.7 (±12.8)	59.6 (±15)	60.3 (±9.2)		
	4	0.4 (±0.1)		2.8 (±0.4)	10.6 (±5.3)	27 (±2)	57 (±15)	67 (±5.6)		
	11					21 (±3)	25 (±6)	49 (±10)		
	17		0.56 (±0.24)	1.6 (±0.6)	4.8 (±1.4)	6.4 (±1.3)		18 (±5)		
Flamborough	0.7			5.1 (±0.6)	5.7 (±1.3)	16.4 (±6.0)	22 (±3)	25.6 (±4.2)		
	4			3 (±1)	7.5 (±2)			42.3 (±7.6)		
	7				4.2 (±2)	9.0 (±2.9)	16.4 (±6.3)	26.6 (±7.8)		
Petticoe Wick Bay	0	0.5 (±0.2)	2.0 (±0.4)	8.9 (±2.6)	21 (±5.8)	45 (±5)	61 (±6)	64 (±6)		
	1	0.25 (±0.2)	1.9 (±0.8)	7.5 (±2.8)	31.7 (±4.6)	59 (±4)	71.6 (±4.2)	89.6 (±6.0)	101 (±18)	105 (±40)
	5	0.125 (±0.03)	0.35 (±0.12)	2.8 (±0.53)	14.9 (±4.5)	77 (±10)	96.3 (±10.3)	111 (±11)	114 (±20)	
	9	0.022 (±0.03)	0.62 (±0.3)	8.8 (±2.2)	22.9 (±2.8)	41 (±4)	60 (±7)	71 (±6)		
	11		0.87 (±0.42)	2.2 (±0.43)	4.6 (±0.45)	6.9 (±1.1)	8.8 (±1.4)	11.3 (±0.8)		

TABLE V

Dry weights of fronds at the peak season at various ages in different populations sampled by Whittick (1969). Fiducial limits at 0.05 shown in brackets. For latitudes and longitudes see Table IX.

Site	Depth m below LAT	Age in years						
		1	2	3	4	5	6	7
Sennen Cove	2			16.5 (±2.5)	37 (±10)	98 (±48)	103 (±31)	107 (±11)
	6				22 (±4)	82 (±4)	100 (±4)	142 (±34)
	9		5.6 (±0.7)	12.5 (±2.5)	23 (±1)	56 (±10)	92 (±17)	117 (±15)
	12			7.5 (±3.2)	17.6 (±5.3)	27.5 (±9.5)	42 (±17)	57 (±17)
Dunmanus Bay	1	1.7 (±0.6)				85 (±19)	122 (±10)	155 (±55)
	4		2.2 (±0.6)		28 (±10)			108 (±12)
	11					33.3 (±3.3)	76 (±11)	90 (±13)
	17		0.8 (±0.6)	1.2 (±0.8)	42 (±4)	10 (±8)		17.2 (±1.8)
Flamborough	0.7			1[illegible] (±4)	15.3 (±4.5)	27 (±8)	43 (±8)	58.4 (±4.7)
	4			4.2 (±1.1)	6.3 (±2.4)			30.8 (±7.9)
	7				8.0 (±3.7)	13.8 (±4.7)	15 (±11)	31 (±8)
Petticoe Wick Bay	0			7.3 (±1.6)	37 (±10)	88 (±10)	114 (±21)	117 (±6)
	1		6 (±1)	45 (±5)	76 (±6)	106 (±11)	123 (±10)	130 (±9)
	9				38.5 (±10)	77 (±11)	64 (±5)	
	11		1.4 (±0.8)	13.6 (±4.2)	20 (±7)	28 (±6)	29 (±5)	36 (±6)

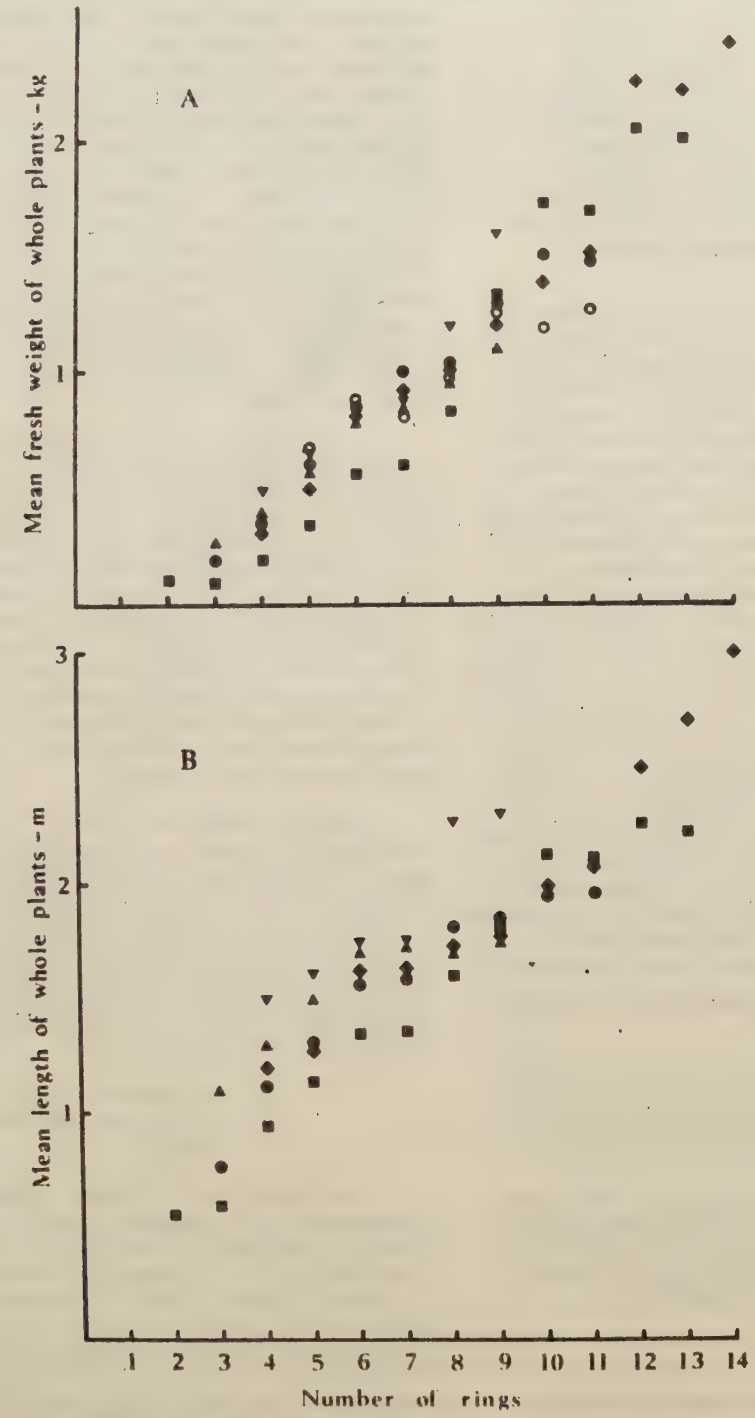


Fig. 12 Measurements of individual whole plants collected from throughout each sampling area with different numbers of rings in the stipe (approximating to age).

A. Mean fresh weight. B. Mean length.

▲, Kvitsøy ▼, Karmøy ◆, Tustna
■, Nord Frøya ●, S. Helgeland ○, E. Finmark

For site positions see Table IX. (Data replotted from Grenager, 1953, 1954, 1955, 1956 and 1964.)

At Yttersiden (Baardseth, 1954) the lengths were 1.6 m (3.4). It seems likely that the maximum length of this plant is reached only between the latitudes of about 55°N and 65°N. Kain (1967) concluded that southwest Norway is at about the optimum latitude for the species. As has been shown, there is little effect of latitude on the size of the plant at any given age and the greater maximum size at the optimum latitude is mainly due to greater longevity (Kain, 1963, 1967).

In most cases, although the stipe varies in appearance under different conditions it does not vary in basic shape. There is a straight line relationship between the logarithm of the stipe weight and the logarithm of the stipe length which is the same for most populations from very different habitats which include deep water and thus low irradiance (Kain, 1971). Figure 13A shows this relationship and incorporates the data from five populations. There seem to be, however, occasional exceptions to this relationship. In some sites, John (1968) found stipes which were abnormally long for their weight. Figure 13B shows plots of age group means of ash-free dry weight against length from a number of sites (John, 1968). Some from polluted water (squares) can be seen to be off the line to the right, particularly in large plants. Here stipes 2 m long have the same weight as stipes 1 m long from most other populations. However, two further populations showed similarly long lengths at these weights, those from off the island of Coll in the inner Hebrides (triangles). Here the water was clear and unpolluted. What causes this effect is thus obscure. There is no evidence that it is due to "etiolation" as suggested by Bellamy and Whittick (1968) because it is not shown in deep water (Kain, 1971a).

4.13 Sporophyte-gametophyte and sex composition

Nothing is known of the density of gametophytes in the field but it is likely that they normally far outnumber the sporophytes which in turn are astronomically greater in biomass.

Schreiber (1930) isolated single unilocular sporangia and found that equal numbers of males and females developed from each. Unless their survival is differentially affected, therefore, the sex ratio of the gametophytes is 1:1.

4.2 Density

4.21 Average densities of defined areas

Most of the surveys of populations of L. hyperborea have been made by the spring grab technique. In this a grab is lowered from a boat and when protruding feet touch the bottom the jaws are closed by powerful springs, the teeth of the jaws either cutting stipes, usually near the rock, or pulling holdfasts off, thus retrieving whole plants. The grab used by Walker in Scotland sampled half a square yard and that used by Grenager in Norway half a square metre (100 x 50 cm or 71 x 71 cm). It is clear that this method must miss some of the biomass and some of the individuals. It may also sample relatively blind. It may land on unsuitable substrata. In expressing density or standing crop from this method there is a choice of averaging the results from all the samples or only those which contained weed. The first alternative would give an artificially low result on a mixed bottom if density on rock is required, while the second alternative may give a high result in deep water where density is low even on suitable rock.

Densities, in terms of numbers of individual plants per square metre, obtained by various authors, either through the use of the spring grab or by diving, are shown in Table VI. It is at once clear that the results obtained by diving are considerably higher than those obtained by the spring grab. This would be expected from the difference in technique. When all the young plants can be collected by a diver the apparent density must be more variable and particularly high when conditions have allowed a plentiful growth of sporelings. The grab data, based on many samples and including mainly mature plants, are much more consistent.

Lüning (1969a) made use of a concept initiated by higher plant ecologists, the leaf area index (LAI), or area of leaf per unit area of substratum. He found an index of 4.1 on a bottom at 2 m below mean low water springs, 2.3 t 3 m and 1.6 at 4 m. The last were thus approaching an open community where there is little self shading. Drach (1949) gave figures equivalent to 6 to 8 for populations in the English Channel.

4.22 Variation in density with ecological and accidental factors

The most obvious factor affecting density is depth. It is apparent from all the observations made at different depths in Table IV that there is a progressive decrease in density in deeper water. This is presumably due to decrease in irradiance, and is more rapid in turbid water such as that around Helgoland. Ernst (1966) found that the total density of a mixture of L. digitata, L. hyperborea and L. ochroleuca in north Brittany decreased logarithmically with depth. It has been suggested (Lüning, 1969a; Kain, 1971a) that the decrease in density, and thus in self-shading, with depth partly counteracts the decrease in irradiance and this results in the amount of light reaching the plants below the canopy being relatively constant with depth, within limits. This could explain the relatively small change in apparent

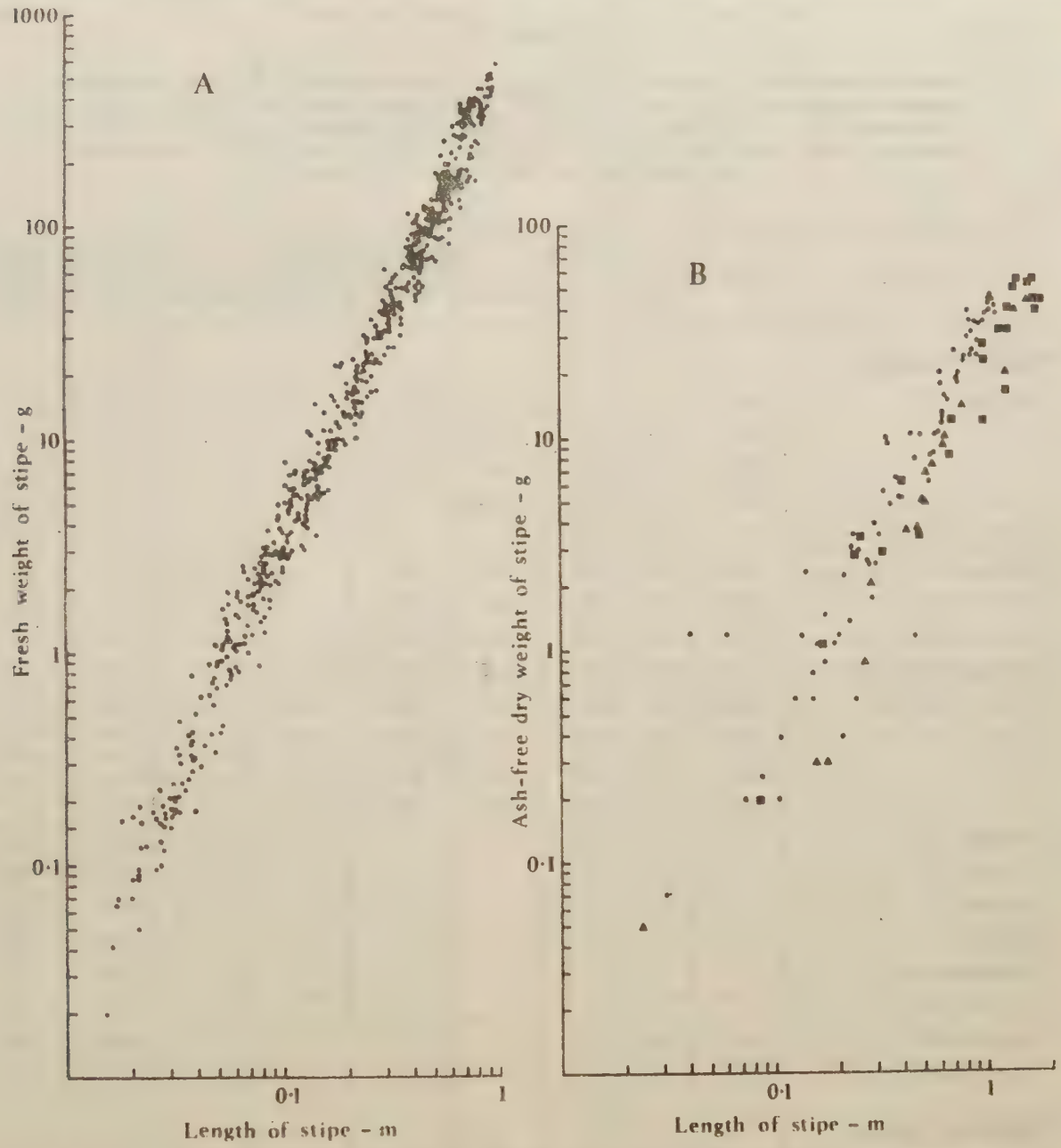


Fig. 13 A. Stipe fresh weights plotted against stipe length for populations MS4, ME4, ME17, BE33, BS18 (see Table IX for positions). (Data mainly from Kain, 1971a.)

B. Stipe ash-free dry weight plotted against stipe length for the following populations:

● , St. Abb's Head 55°54-5'N, 2°8-9'W; Beadnell 55°33'N, 1°37'W; Saddell Bay 55°32'N, 5°30'W; Rubh'n Amair 55°46'N, 5°5'W; Cardigan Island 52°8'N, 4°42'W; and Sennen Cove 50°5'N, 5°41'W.

■ , Marsden 54°58'N, 1°21'W; and Redcar 55°38'N, 1°2'W.

▲ , Coll 56°34'N, 7°39'W.

(Data from John, 1968.)

TABLE VI

Density, as number of plants of L. hyperborea per square metre at various depths sampled by Walker (1), 1950, 1952, 1957; Walker and Richardson (2), 1955, 1957; Grenager (3), 1953, 1954, 1955, 1956, 1958, 1964; Bellamy et al. (4), 1968; John (5), 1968; Whittick (6), 1969; Lüning (7), 1969a; and Kain (8) unpublished. For latitudes and longitudes see Table IX.

Locality	Year	Plants/m^2 in samples with weed						Mean–all depths	
		0–2m	2–6m	6–10m	10–14m	14–18m	18–22m	With weed	All samples
Obtained by grab:									
Girvan (2)	1952							7.8	
	1953	8.6	7.0	5.5	2.4				
	1954	9.4	9.9	6.5					
	1955	9.1	8.3	5.2					
Ailsa Craig (1)		7.4	6.6						
Dunbar (1)	1952	5.6	5.8	4.3	3.4			5.2	
(2)	1954	9.1	7.3	4.6	3.2				
(2)	1955	8.8	7.7	6.1	4.6				
NE May Island (1)		16.3	10.5	9.0	8.0				
Fraserburgh (2)	1952	4.8	6.2	6.0	4.4	3.2		5.6	
	1953	6.2	7.5	6.0	4.5	3.0			
	1954	7.0	6.8	6.2	5.4	4.5			
	1955	7.6	9.0	9.1	6.8	5.5			
Kvitsøy (3)								9.3	8.6
Karmøy (3)								9.6	8.8
Tustna (3)								8.3	7.9
Sula (3)								9.4	9.3
Frøyene (3)								8.4	7.8
S. Helgeland (3)								7.7	7.5
Helgøy (3)								5.7	3.4
E. Finmark (3)								6.1	2.7
Obtained by diving:									
Sennen Cove (4)			27	38	42		12		
Helgoland (7)		27	12						
Flamborough (6)		16	10	5					
Isle of Man (8)		27	39						
Petticoe Wick Bay (5)			34	23					
(6)		20	23	17	6				
Connel Sound (8)	1970		23	17					
Muldoanich Is. (8)	1970			46		14			
Off Loch Boisdale (8)	1970						0.2		

growth rate with depth under forest conditions (see 4.12).

Another factor affecting density may be latitude. There is no general trend apparent from Table IV but it is possible that densities are lower near the northern limit of the species, particularly if all the samples and not just those with weed are considered. This is supported by Kain's (1967) observation that apparently suitable substrata are weakly colonized by L. hyperborea in north Norway. One would expect this of any plant near its geographical limit but it would be unwise at present to guess the critical factor involved.

There is evidence that in some areas grazing can affect the density of this species. Jones and Kain (1967) regularly cleared Echinus esculentus off an area of rock at 10 m below LAT normally bare of laminarians and an algal population developed which after two years included a mean density of L. hyperborea of 4.4 plants/square metre.

4.3 Mortality, morbidity

The maximum age of plants in the Isle of Man so far found by Kain is ten years. In the Norwegian populations studied by Kain (1971a) the maximum age was 11 years but larger samples could have revealed older plants. Grenager certainly found plants with more rings though, as already mentioned, these may not be very reliable as indications of age. However, as some of his plants were very large and his samples numerous, it is possible that all the rings represented years. The highest was 18 in E. Finmark (Grenager, 1956). He also recorded 16 in Nord-Frøya, 15 in Jøssund (Grenager, 1964), 15 in S. Helgeland (Grenager, 1955), 14 in Tustna (Grenager, 1954), 13 in Karmøy and 12 in Kvitsøy (Grenager, 1953).

This perennial species shows no obvious mechanism for the decay of any part of the individual or for obvious senility of the whole. The old frond is shed after about a year but this is probably a mechanical process rather than a progressive degeneration as in some species of the genus. Nor does the whole plant cease its capability for growth after a limited period as do some genera in the order. The capacity for growth may be reduced after some years but as long as the plant remains intact, attached and the conditions remain suitable, new tissue seems to be produced each growing season.

Amongst outside factors the most obvious cause of death is physical removal of a plant from the substratum. The force causing this removal is likely to be wave action or other water movement, while that resisting it is the power of adhesion of the holdfast in relation to the size of the plant. Although this adhesion is greater where there is water movement (see 1.31), and the size and extent of the holdfast increases with the size of the plant, there must come a stage in the development of a plant (except under very sheltered conditions) when the attachment is inadequate to hold its bulk against the movement of the water. This explains why plants at 1 m in the Isle of Man have a lower longevity than those at 2 m or more, because wave action is most severe near the water surface. Anything that decreases the efficiency of the attachment mechanism must increase mortality. Kitching (1937) concluded that just above low water springs attachment to barnacles instead of rock surface subsequently led to breaking away, but this is unlikely to be important in deeper water because barnacle cover is less dense. In much of Britain a serious cause of weakening of the holdfast is grazing by Patina pellucida which eats cavities in the base of the stipe and detaches it from many of the haptera. The chances of infestation seem to vary from place to place. In the Isle of Man they are high, with all age groups above one-year olds affected, and at 1 m below LAT the mean infestation of five to seven-year olds was 54 percent (Kain and Svendsen, 1969). In Berwick, southeast Scotland, however, in a large sample from 0 to 5 m no two or three-year olds were infested and the mean infestation in the same age range was only 14 percent (Whittick, 1969). In both cases infestation increased with age up to seven years and then dropped, suggesting an effect on mortality. Many examples of broken holdfasts without stipes with Patina cavities have been seen in the Isle of Man. However, although Kitching (1937) found that 90 percent of the L. hyperborea plants washed up on the beach near Plymouth (southwest England) after storms had been detached at the holdfast, only a few of them were infested with Patina. This, therefore, seems an area of lower risk than the Isle of Man. John (1968) also found relatively low infestation levels in sites in northeast and southwest England and west Scotland, with a mean of eight percent in five to seven-year olds. However, his data included all depths and sites. There is evidence that infestation decreases with depth (Vahl, 1971). It is known that there is a change in behaviour of the limpet with latitude. In France (Sauvageau, 1918), southwest England (Graham and Fretter, 1947), the Isle of Man (Kain, 1963) and southeast Scotland (Whittick, 1969) it penetrates the holdfast but it does not in parts of west Scotland (Kain, unpublished) or Norway (Kain and Svendsen, 1969). This may partly explain the apparent greater longevity of L. hyperborea in Norway than in the Isle of Man.

Before the holdfast becomes inadequate to hold a plant in the prevailing conditions some other accident may have befallen it. Possibly the most likely is grazing by an echinoid. Near their area cleared of Echinus esculentus, Jones

and Kain (1967) found that, although in July sporelings of L. hyperborea had developed on boulders at 10 m up to a density of 20 plants/square metre, by November almost all had disappeared except where clearance continued. Thus Echinus was responsible for the destruction of many sporelings of less than 100 mm. It is likely also that Echinus can damage mature plants irreparably. The animals are frequently to be seen grazing on the plants or their epiphytes, and when this is extensive at the transition zone recovery may be impossible. Patina may also damage this vulnerable region (Kain and Svendsen, 1969). However, stipes are frequently found broken further down and the reason for this is not apparent though it can be caused by the plant becoming entangled and the stipe bent sharply for a period. On fertile fronds Patina frequently grazes on the sorus, destroying the sporangia. Another grazer which may be important in Norway is Lacuna vincta (Vahl, unpublished). Vahl found considerably higher densities of this gastropod than of Patina at Lyrrodane in Norway and the holes it makes are deeper.

It seems unlikely that fronds are regularly grazed by fish. One sparse population of plants was found in the Isle of Man with their fronds partly eaten (Kain, unpublished). This was in a region of fairly fast tidal stream and subsequent observation showed that in many cases the fish Labrus bergylta was stationed downstream of each plant apparently using it as cover. The fish snapped at food passing in the current and, because the frond was waving about in front of it, occasionally took a bite out of it. This sort of damage is unlikely to be important in mortality.

Diseased plants have sometimes been observed. Fronds of the population BS4 in Norway (Kain, 1971a) were blackened at their tips and were decaying but the causative agent was not identified.

4.4 Total quantities (standing crop) of defined areas

Surveys of the standing crop of L. hyperborea have been made almost exclusively using the spring grab (see 4.21). Unfortunately Walker always used the term "density" for the fresh weight per unit area instead of its more usual use for the number of individuals per unit area. Again there is a choice of expressing the results using all the samples or only those which contained weed. In Table VII the data have been selected or recalculated from samples with weed, this being more realistic in shallow water but perhaps less in deeper water. The only samples in the table obtained by diving are those of Lüning from Helgoland. They are comparable to the grab samples instead of being much higher as were his density figures. As a grab is more likely to miss small plants than large, more difference would be expected between the two methods in terms of numbers than of weights. However, when Grenager (1956) and Baardseth (1954) cleared quadrats by hand they obtained 1.5 to 3 times as much fresh weight in kg/m^2 as obtained by the grab technique.

In most cases, as expected, there is a decrease of standing crop with depth (Table VII) and thus with irradiance. Walker (1954) stated that this decrease was more the result of a reduction in density (individuals/unit area) than of weight of individual plants. This was confirmed by Lüning (1969a). This does not mean, of course, that there is no decrease in plant size with depth, because this has been shown to be the case in some instances (Kain, 1963, 1967; Lüning, 1970a; John, 1968; Whittick, 1969) but this is unimportant from the point of view of standing crop, compared with density decrease.

Considerable differences were found by Walker when he repeated some surveys in areas in Scotland. In one case, at Dunbar, this was probably due to accumulation of sand (Walker and Richardson, 1955). Taking the surveys shown in Table VII, which included only L. hyperborea and in addition further surveys and their repeats including also L. digitata and L. saccharina, Walker (1956a) found that there was a general trend in standing crop from a peak in 1947 to a trough in 1953. This he later correlated with sunspot activity (1956b). There has been no confirmation of this somewhat unlikely possibility.

The total standing crop of stretches of coast where L. hyperborea was almost exclusively dominant is shown in Table VIII. Chapman's (1948) figures were based on a somewhat hurried war-time survey using a grapnel and echo-sounder from a boat and aerial photography. Walker and Richardson's and Grenager's figures were the result of surveys with the spring grab previously mentioned. Boney (1965) compared Walker's and Chapman's data for total Laminariaceae and concluded that more detailed mapping results in higher estimates. In his surveys Walker usually applied the following formula to his results and obtained values for k and ϒ according to the site:

$$\frac{\sqrt{d}}{C} = k - \gamma f$$

where d = fresh weight of weed per unit area in all samples,

C = % samples containing weed,

f = depth.

(Walker and Richardson, 1955.)

TABLE VII

Standing crop, as kilogramme of fresh weight of L. hyperborea per square metre at various depths sampled by Walker (1), 1950, 1952, 1957; Walker and Richardson (2), 1957; Grenager (3), 1953, 1954, 1955, 1956, 1958, 1964; Baardseth (4), 1954; and Lüning (5), 1969a. See Table IX for latitudes and longitudes.

Locality	Year	kg/m² in samples with weed							
		0–2m	2–6m	6–10m	10–14m	14–18m	18–22m	22–26m	26–30m
Obtained by grab:									
Girvan (2)	1952	8.0	7.0						
	1953	6.2	5.3						
	1954	5.3	5.3						
	1955	5.5	5.0						
Ailsa Craig (1)	1955	5.7	3.5						
Dunbar (1)	1949	6.7	5.3	3.4	0.9				
(2)	1952	3.6	3.4	2.1	1.1				
(2)	1954	5.0	3.6	2.0	1.0				
(2)	1955	5.0	4.2	1.8	1.0				
NE May Island (1)	1956	5.5	2.9	1.7	0.9	0.8			
Fraserburgh (2)	1952	3.3	4.5	4.0	2.2	1.0	0.7		
	1953	3.1	3.6	2.9	1.6	0.9	0.8		
	1954	4.4	4.3	3.3	2.7	1.8	2.0		
	1955	3.4	3.8	3.2	2.2	1.3	1.2		
Holm Sound, Orkney (1)	1948	5.9	5.6	4.4	3.4				
Sanday Sound, Orkney (1)	1947	7.3	7.0	6.1	3.8				
E. Sanday, Orkney (1)	1948	7.1	7.7	7.3	6.4				
N. Sanday, Orkney (1)	1948	7.1	7.7						
Kvitsøy (3)	1952		8.8	5.2	3.6	3.4	1.0	0.2	
Karmøy (3)	1952	7.6	9.8	7.8	4.2	4.2	0	0	
Tustna (3)	1952–3	8.6	9.0	9.0	6.0	5.4	3.4	1.9	1.2
Sula (3)	1954	12.6	10.0	10.0	5.0				
Frøene (3)	1954	12.0	9.2	6.8	4.8	1.2	0.6		
S. Helgeland (3)	1952–3	9.0	9.0	8.2	4.4	4.2			
Røst (4)	1952		6.9	4.3					
Karlsøyvaer (4)	1952	5.4	5.9	3.5	3.9	1.1			
Nordlandsflaket (4)	1952		5.2	2.0	3.6	2.2	2.0		
W. Moskenesøy (4)	1952	6.8	7.8	7.4	3.4	2.7	1.6		
E. Moskenesøy (4)	1952	6.1	6.8	5.2	3.5	2.4	1.7	0.6	
Vitken (4)	1952		3.5	3.0	3.1	2.2	1.5		
Helgøy (3)	1953		7.4	6.0	4.8	3.6	1.9	1.7	0.2
E. Finmark (3)	1953	5.16	7.38	6.1	3.88	2.4	2.4	0.2	
Obtained by diving									
Helgoland (5)		8.7	4.7						

TABLE VIII

Estimated standing crop of weed on surveyed sections of coast dominated by L. hyperborea at all depths. Data from Chapman (1) 1948; Walker (2), 1950, 1952; Walker and Richardson (3), 1955; Grenager (4), 1953, 1954, 1955, 1958, 1964; and Baardseth (5), 1954. See Table IX for latitudes and longitudes.

Locality	Area km^2	Standing crop Metric tons (Mg)
Berwick/Newbiggin (1)		119 600
Dunbar (2)	13.8	51 400
St. Andrews (1)		43 800
Balintore (1)		53 200
Halmsdale (1)		60 600
Sound of Barra/W. Loch Tarbot (1)		682 000
Fraserburgh (3)	2.93	11 700
Holm Sound, Orkney (2)	5.3	19 800
Sanday Sound, Orkney (2)	26.3	107 200
E. Sanday, Orkney (2)	19.4	129 000
Kvitsøy (4)	9.7	65 000
Karmøy (4)	10.6	76 000
Tustna (4)	7.0	60 000
Sula (4)	25	250 000
Froøene (4)	20	140 000
S. Helgeland (4)	49.3	312 000
W. Moskenesøy (5)	3.04	14 000
E. Moskenesøy (5)	1.96	7 000
Vikten (5)	22.25	46 000
Helgøy	100.6	281 000

4.5 Accompanying species

Over most of its geographical range L. hyperborea is the longest lived dominant species. This explains its success in competition with faster growing examples of Laminariales. Once it has become established the high canopy formed by the fronds effectively excludes almost all serious competition. The species with which it competes for establishment are all members of the Laminariales. In sites with very severe wave action Alaria esculenta is successful in shallow water.

Just above low water springs where wave action and exposure to air are not too severe, it is L. digitata which succeeds in place of L. hyperborea. Under sheltered conditions north of the English Channel L. saccharina may dominate as it does also on unstable boulders which may be turned over without damage to its flexible stipe. From the English Channel southward L. ochroleuca is a serious competitor in slightly sheltered sites. This species, similar in habit to L. hyperborea, is co-dominant with it in many places where their geographical ranges overlap (John, 1969) and replaces it in shallow water in Spain (Seaone Camba, private communication). Finally, L. hyperborea competes with opportunists in situations where the substratum is temporarily denuded. The most successful of these south of Norway is Saccorhiza polyschides. Other brown algae such as Desmarestia viridis, D. aculeata and even Alaria esculenta and Laminaria saccharina can act as opportunists and dominate for a period in sites

TABLE IX

Latitudes and longitudes of sites in previous tables

Site	Latitude	Longitude
Ailsa Craig	55°16'N	5°7'W
Balintore	57°15'N	3°55'W
BCu0.5	60°19'N	5°16'E
BE4	60°9'N	5°7'E
BE33	60°9'N	5°7'E
Berwick/ Newbiggin	55°47'N 55°12'N	2°W 1°30'W
BH14	60°10'N	4°59'E
BS4	60°10'N	5°E
BS18	60°16'N	5°13'E
Connel Sound	56°28'N	5°24'W
Dunbar	55°57'N	2°24'W
Dunmanus Bay	51°35'N	9°45'W
E. Finmark	70°21'N	31°7'E
E. Moskenesøy	67°58'N	13°10'E
E. Sanday	59°16'N	2°30'W
Espevaer	59°30'N	5°6'E
F2	54°4-5'N	4°46-7'W
F5	54°3-5'N	4°46-7'W
Flamborough	54°8'N	0°5'W
Fraserburgh	57°42'N	2°4'W
Frøyene	64°2'N	8°54'E
Girvan	55°10'N	4°57'W
Helgoland	54°10'N	7°55'E
Helgøy	70°12'N	18°50'E
Helmsdale	58°7'N	3°40'W
Holm Sound	58°52'N	2°52'W
Isle of Man	54°5'N	4°46'W
Karlsøyvaer	67°33'N	14°50'E
Karmøy	59°16'N	5°6'E
Kvitsøy	59°3'N	5°25'E
L5	54°4-5'N	4°46-7'W
L10	54°3-5'N	4°46-7'W
Loch Boisdale	57°9'N	7°15'W
May Island	56°12'N	2°32'W
MCa4	54°7'N	4°44'W
ME4	54°5'N	4°46'W
ME14	54°3'N	4°47'W
ME22	54°3'N	4°46'W
MS4	54°6'N	4°45'W
Muldoanich Island	56°55'N	7°26'W
Nordlandsflaket	67°45'N	12°45'E
N. Sanday	59°18'N	2°32'W
Petticoe Wick Bay	55°55'N	2°9'W
Reine	68°0'N	13°0'E
Røst	67°30'N	12°10'E
St. Andrews	56°20'N	2°18'W
Sanday Sound	59°12'N	2°40'W
SE6	57°44'N	5°47'W
SE10	57°44'N	5°48'W
SE16	57°7'N	5°48'W
Sennen Cove	50°5'N	5°25'W
S. Heigeland	65°25'N	11°45'E
Sound of Barra/ W. Loch Tarbot	57°5'N 57°55'N	7°25'W 7°W
SS5	55°42'N	4°57'W
Sula	63°50'N	8°25'E
TE2	69°36-55'N	18°1-43'E
Trondheimsfjord	63°30'N	10°30'E
Tustna	63°11'N	7°55'E
Vardö	70°20'N	31°0'E
Vitken	68°58'N	13°15'E
W. Moskenesøy	67°57'N	12°55'E

where the climax vegetation is dominated by L. hyperborea.

The algal species forming the undergrowth to an L. hyperborea forest vary somewhat with the latitude. On the French coast of the English Channel, the Channel and Scilly Isles, the following species are common in the undergrowth (Drach, 1949; Ernst, 1955; Kain, 1961; Norton, 1968): Callophyllis laciniata, Delesseria sanguinea, Cryptopleura ramosa, Phycodrys rubens, Plocamium cartilagineum, Pterosiphonia parasitica, Dictyota dichotoma, Phyllophora crispa, Kallymenia reniformis, Dilsea carnosa, Heterosiphonia plumosa, Halopteris filicina and Dictyopteris membranacea. Though none of these species is absent from the Isle of Man only the first eight are common in the undergrowth there, but additional common species are Cutleria multifida sporophyte, Odonthalia dentata and Desmarestia aculcata (Kain, 1960). All these species are also common in west Scotland (McAllister et al., 1967). Missing from this list in Helgoland are Callophyllis, Cryptopleura, Pterosiphonia, Cutleria and Odonthalia (Lüning, 1970b). However, a number of other species are relatively more common: Phyllophora membranifolia, Corallina officinalis, Ulva sp. In southwest Norway the only absentee of the species common in the Isle of Man is Cryptopleura. However, neither Plocamium nor Pterosiphonia are common there (Breivik, 1958; Jorde, 1966). In north Norway most of these species are absent but Phycodrys, Ptilota plumosa, Desmarestia aculeata and D. viridis are abundant (Jaasund, 1965). Delesseria and Odonthalia are also present.

Drach (1949) estimated that in an L. hyperborea forest of a density of 20 plants per square metre, the area suitable for settlement, provided by the rugose stipes of this species, could be 150 percent of the rock surface. This additional habitat is particularly favourable to plants because they receive more light than on the rock surface. Tokida (1960) lists records of epiphytes on L. hyperborea stipes and fronds totalling 71 species. Many of these are chance inhabitors and the main occupants of the stipes are fairly constant in any one locality. Marshall (1960) and Whittick (1969) studied the epiphytes of L. hyperborea stipes in Berwick, southeast Scotland and both found that four species were of particular importance. Rhodymenia palmata was confined to shallow water and the distal part of the stipe while Phycodrys rubens was more important in deep water. Ptilota plumosa and Membranoptera alata were mixed with or slightly distal to Phycodrys. On the other hand Lüning (unpublished) reports that Polysiphonia urceolata and Membranoptera alata are the only abundant stipe epiphytes in Helgoland. Whittick (1969) found that the epiphyte biomass was greatest at 1 m below LAT, showed a seasonal peak in September and increased with the age of the host up to five years. Whittick (1969) also observed sites in Yorkshire, southwest Ireland and extreme southwest England. In all Ptilota was absent and Rhodymenia extended deeper. In southwest England there were no epiphytes below 22 m although L. hyperborea extended to 36 m. Kitching (1941) found Delesseria sanguinea, Odonthalia dentata and Cryptopleura ramosa abundant on stipes in west Scotland and Marshall (1960) also found that Plocamium cartilagineum, Pterosiphonia parasitica, Callophyllis laciniata, Ptilothamnion pluma and Plumaria elegans fairly common in southeast Scotland. Except for Odonthalia, Cryptopleura, Ptilothamnion and Plumaria all these species (in addition to others) were found on stipes in Nørd-Frøya (64°N) in Norway (Grenager, 1964). On the other hand, Jaasund (1965) lists as epiphytes only Rhodymenia palmata, Polysiphonia urceolata, Odonthalia dentata, Euthora cristata (on haptera), Ectocarpus fasciculatus (on fronds) and Phloeospora curta (Foslie) Jaasund (on fronds). E. fasciculatus is also common on old fronds in the Isle of Man (Russell, 1966), along with Giffordia hincksiae (Russell, private communication) and Laminariocolax tomentosoides (Russell, 1964).

Sloane et al. (1957) investigated the animals inhabiting the fronds of L. hyperborea near Lough Ine in southwest Ireland. The commonest was Patina pellucida, followed by Membranipora membranacea and Obelia geniculata. Also recorded were Hippothoa hyalina, Sertularia operculata, Scruparia chelata, Hiatella arctica and anomiids.

The holdfast of L. hyperborea forms a home to a great many animals, far too numerous to list. For example, Moore (1971a) found 387 species in holdfasts collected only from the northeast coast of Britain from Berwick to Yorkshire. Of 61 species of nematodes, five were regularly abundant (Moore, 1971b).

5 HARVESTING

5.1 Equipment and methods of harvesting

The simplest method of harvesting, which has been used for centuries, is the collection of cast weed. This is the only method used in Britain now. Sickles have sometimes been used to cut weed at low water.

Grapnels can be used from boats to haul in plants of L. hyperborea. The normal boat grapnel with prongs curving inward from the end of the shaft is less effective than a specially designed instrument with prongs curving outward from an acute angle (Chapman, 1944). Chapman found that a diamond-shaped instrument was better still. In Scotland, at what was later called the Institute of Seaweed Research, another type was developed but found inadequate for commercial harvesting (Jackson, 1942).

In further work at the Institute, the continuous grapnel (Hay, 1952), later called the belt harvester (Jackson and Wolff, 1955; Jackson, 1957), was developed. This consisted of a conveyor belt of flexible wire mesh and chains at the edges with rows of hooks across at intervals. The weed was compacted by the mesh, torn off by the hooks and carried up to the boat on the belt. This system was tried out extensively and seemed to be fairly satisfactory though its depth range is clearly limited. It is not in commercial use.

Another method on which the Institute worked consisted of using a cutting head (Jackson and McIver, 1952) in the weed bed and sucking it up to the boat in a flow of water (Jackson and Macduff, 1952). They had difficulty in controlling the entry of the weed into the pipe and although this problem was solved in a test tank (Jackson, 1957), the developed suction method was never finally tried out in the sea and is not used commercially.

The only apparatus in commercial use is the "trawl". This term is incorrect because the apparatus has a rigid lower boundary to the mouth and should thus be called a dredge (Davis, 1958). One of the earliest of these was used by the Institute of Seaweed Research to secure nearly whole plants (Jackson, 1949). It consisted of an open-ended rigid box with rows of triangular knives at the mouth. It was used little because the knives became clogged. Another dredge, which was used commercially for some years in Norway, is described by Smörholm (1964) and Svendsen (in preparation). This also consisted of an open-ended box 1.5 m long, its floor being a plate of steel and the sides and roof of wire mesh with a row of triangular knives at the lower edge of the mouth. It was set on runners to raise the knives off the bottom and had a float on the wire case. It worked best between 0 and 5 m and had a capacity of 380 kg (fresh weight). A much larger dredge ("trawl"), collecting 1 000 kg, with a horizontal knife, is now in regular use in Norway.

A number of experimental approaches to the problem of drying L. hyperborea have been made. About half the water was found to be removable without heating by Reid and Jackson (1956). The mechanical methods which they employed were centrifuging after hammer-milling, batch pressing, squeeze rolling and screw expelling. Detailed investigations have been made of thermal through-circulation drying of the stipe (Gardner and Mitchell, 1953a) and the frond (Gardner and Mitchell, 1953b). The material had to be cut fairly fine for this method to be economical. The design of through-circulation dryers was summarized by Gardner and Mitchell (1956). What was claimed to be a more economical method of drying this species was described by Booth (1956). Milled fresh material is poured between two parallel steam-heated drums rotating in opposite directions in such a way that it is squeezed into a thin layer as it moved downward between the two drums, adheres to each, is dried quickly on the surfaces and is scraped off before a full revolution of the drum takes place.

In practice L. hyperborea is treated in Britain as follows. Stipes cast up on the shore are collected and air-dried locally in stacks. Fronds are not used. The half-dried stipes are sent to South Uist (Outer Hebrides, Scotland) where they are further dried in batches on iron tip-wagons in a heating chamber through which hot air is circulated. The material is then milled to a meal and sent to an alginate factory in west Scotland.

In Norway, on the other hand, this species is actively harvested in situ. Most of the material is collected from fishing vessels or from specially designed boats, using a dredge ("trawl") as already described. The weed is cut off above the holdfast by the knife at the leading lower edge and the plants pass into the rigid box and accumulate at the back. When full the dredge is hauled up and emptied into the boat. Either the material is sent to a factory within hours or it is chopped, mixed with formalin and acid and packed into a silo, of which a number are distributed along the Norwegian coast. The material is later transported to the alginate factory in southwest Norway.

5.2 Harvesting seasons

In Britain, because only cast-up stipes are used, harvesting is mainly in the winter when there are most gales and thus strong wave action removing plants from the rock.

In Norway dredging takes place throughout the year but, again because of strong winds in

winter (in this case unfavourable), the best seasons are spring, summer and early autumn.

5.3 Harvesting areas and depths

British supplies come from west Ireland (Flood, 1953), the Outer Hebrides, the Orkney and the Shetland Islands. Presumably plants from all depths within its range of growth are included in the cast.

In Norway harvesting takes place on the west coast between Jaren (ca 59°N) and Trondelag (ca 65°N). Some hand collection takes place down to 1 m below low water. A small dredge is used from 1 to 5 m and the larger one from 5 to 15 m.

5.4 Regrowth on harvested areas

The first direct observation on regrowth was made by Kitching (1941). He cut forest with shears and found that one year later the remaining holdfasts had disappeared and there was a dense growth of new plants of L. hyperborea with a total height of about 1 m.

Svendsen (unpublished) has observed an area in Norway off Vevang (63°N, 7°16'12"E) which had been harvested at a depth of 2 to 5 m with the seaweed dredge ("trawl", see 5.1), which leaves holdfasts and small plants intact. The standing crop (fresh weight) after 2, 3, 4, 6 and 7 years was respectively: 6 to 10, 12 to 23, 15 to 31, 25 to 38 and 22 to 33 kg/m^2. As he observed values of 20 to 50 kg/m^2 in virgin forest the standing crop had returned to its original level in about five years. However, a maximum stipe length of 2.44 m was observed in the forest and a length of 1.4 to 2.3 m was only attained after six years on the harvested areas. This rate of growth was very fast under these optimal conditions where competition from opportunists seems to be less than in the Isle of Man.

5.5 Total annual yields

Because of the secrecy adopted by the alginate producers precise data on the total quantities harvested are not available. It is probable that in Britain and Norway together a total of just under 4 000 tons of alginate are produced from L. hyperborea each year. As the weight of alginate produced is about 6 percent of the original fresh weight of the algae, this corresponds to a total annual crop of about 60 000 tons of fresh L. hyperborea. Clearly this varies from year to year, particularly in Britain where it depends on the amount cast up. Based on Norwegian prices in 1971, the total value of this crop at first hand corresponds to about £200 000.

6 PROTECTION AND MANAGEMENT

6.2 Control of physical factors

The only obvious way to create a habitat suitable for L. hyperborea is to provide a suitable solid substratum where none existed before. An accidental example of this is Port Erin breakwater in the Isle of Man. This was built in the nineteenth century on sand at about 10 m below LAT and was soon pushed over in a storm. It is now an untidy strip of concrete blocks and boulders 230 m long and 70 m wide, rising from 10 m to about mid-tide. It forms an admirable substratum for L. hyperborea over much of its area, where before there was only sand.

6.4 Control of biological features

6.41 Control of predation and competition

One of the most serious predators of L. hyperborea is Echinus. This can be removed or destroyed by hand by divers but this is a tedious and costly process. The method used for sea urchin destruction in the programme to improve the Macrocystis habitat is the dissemination of quicklime, CaO (Leighton et al., 1966). It is claimed that echinoids are the most sensitive organisms to this substance. A concentration of 0.5 kg/m^2 is allowed to trickle from the stern of a boat moving along a grid and the chemical is distributed by the propeller turbulence. The particles should be large so that they sink quickly and make contact with the urchin before the reaction with water is completed.

There is at present no known method of controlling predation by Patina pellucida.

6.5 Artificial culture

In laboratory culture work the emission of zoospores from fertile fronds of L. hyperborea is fairly easily induced. A fertile frond, preferably with some sign of dehiscence at the tips (greenish patches) is removed from the sea, drained and put straight into a polythene bag which is left overnight in a cool place. Suitable fertile parts of the frond are then cut up and placed in sea water. If emission does not occur within 30 minutes it may be stimulated by a rise in temperature but not above 20°C.

Lüning has used two methods of transplanting this species for experimental purposes. In one (Lüning, 1970a) he left polypropylene ropes attached to iron frames near L. hyperborea plants in January. After some months sporophytes had developed on the ropes which were cut into pieces and attached to P.V.C. plates mounted on an iron frame. The new haptera of the algae soon attached them to the plates. In another method (Lüning, 1969b) he carefully removed plants already growing on the rock, placed them on P.V.C. plates and held them there with a nylon network and rubber bands. Outgrowths of the existing haptera soon attached the plants and the network and bands could be removed before the outgrowth of new haptera above them.

Svendsen and Kain (1971) also transplanted individuals from one site to another. The holdfast was removed from rock and lashed to a stone with thin nylon rope. The stone was placed in a bed of cement mixed with rapid hardener which had been taken underwater in a polythene bag.

John (1968) transplanted first year plants on to underwater frames by enclosing their holdfasts in longitudinal slits in polythene tubing and binding the tubing with thin polythene rope as close to the holdfast as possible.

7 CHEMICAL COMPOSITION

In common with other species of the genus, L. hyperborea has a high content of carbohydrates and mineral matter. There are appreciable differences in chemical content between the stipe and the frond. The stipe is fairly constant in its chemical composition throughout the year, while the frond undergoes marked seasonal variations.

Comprehensive studies on the chemical composition of L. hyperborea have been carried out by the Institute of Seaweed Research in Scotland and by the Norwegian Institute of Seaweed Research. Further references can be gained from the series of publications from each institute and in Levring et al. (1969).

7.1 Water content

Because most chemical analyses of algae are expressed in terms of percentage of dry weight, the fresh weight has not often been determined at the same time so the dry weight as a percentage of fresh weight, or inversely the water content, has rarely been reported. Because of adhering water, fresh weight can clearly be variable according to the technique used to determine it. To avoid drying out of the plant, it should be removed from sea water immediately prior to weighing and shaken to eliminate as much as possible of the surface water (Baardseth and Haug, 1953).

In Figure 14a the dry weight as a percentage of the fresh weight, or inversely the percentage water content, is shown for the frond as it varies with season (Black, 1948a; Black and Dewar, 1949; Black, 1950a). There is clearly a maximum water content of about 87 percent in May and a minimum of about 70 percent in October. This maximum occurs near the end of fast growth when the frond has almost maximal surface area and minimal storage material, while the minimum occurs at the end of the summer assimilatory period when reserves are highest.

As seen from Figure 14b, stipes are less variable in water content, differing little from 85 percent (15 percent dry matter) throughout the year (Black, 1948a; 1950a). Older stipes tend to have more dry matter than younger stipes (Black et al., 1959).

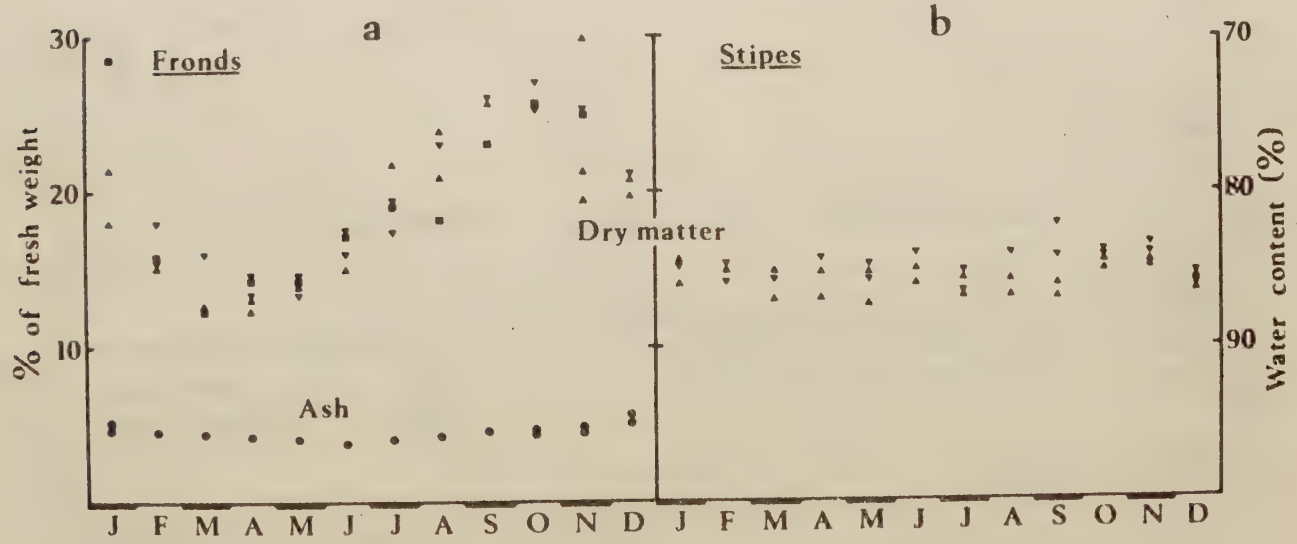


Fig. 14 Total dry matter expressed as a percentage of fresh weight, or water as a percentage of fresh weight (right hand scale), in L. hyperborea fronds (a) and stipes (b).

● , Ash expressed as a percentage of fresh weight in fronds. Data replotted from:

▲ , Black (1948a)

■ , Black and Dewar (1949)

▼ , Black (1950a)

● , Jensen and Haug (1956)

7.2 Inorganic constituents

The total ash left after incineration and expressed as a percentage of the dry matter is shown for the frond in Figure 15a and and stipe in Figure 15b (Black and Dewar, 1949; Black, 1950a; Haug and Jensen, 1954; Jensen and Haug, 1956). Again there is considerable seasonal variation in the frond (from about 15 percent in autumn to about 35 percent in spring) though much less in the stipe (32 to 40 percent). This percentage variation is mainly due, however, to variations in the total dry matter and if the total ash of the frond is expressed as a percentage of the fresh weight as in Figure 14a (Jensen and Haug, 1956), it is shown to be remarkably constant.

Early data on the composition of the minerals in L. hyperborea were collected by Vinogradov (1954). Haug and Jensen (1954) and Jensen and Haug (1956) followed the seasonal change in iodine concentration and in four populations from different sites found a mean minimum of 0.34 percent of total dry matter in fronds and 0.48 percent in stipes and a mean maximum of 0.77 percent in fronds and 0.86 percent in stipes. The levels were rather variable and the minima and maxima not confined to autumn and spring. Larsen and Haug (1961) found that peripheral and older stipe tissue were higher in iodine. Typical contents of some inorganic constituents of spring and autumn samples of fronds and stipes are given in Table X (Jensen, unpublished).

Some determinations of trace elements in L. hyperborea are shown in Table XI. Those by Black and Mitchell (1952) are means of three measurements on material from fronds collected in January and May. Those by Lunde (1970) of fronds from Reine are means of six determinations at two-monthly intervals. The only elements showing regular variation with season were arsenic, zinc and antimony, all lower from June to October than in the other months. There seem to be considerable differences in the levels reported by the two separate authors.

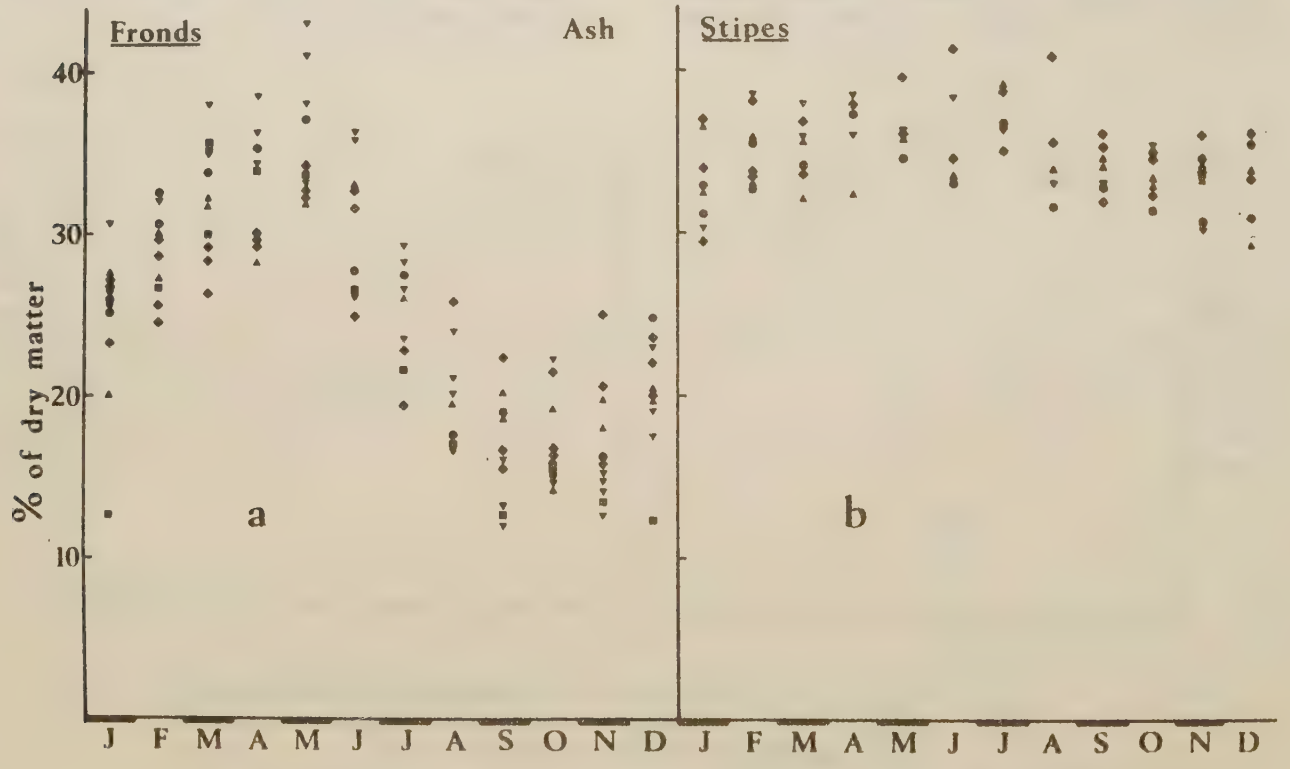


Fig. 15 Ash expressed as a percentage of dry matter in L. hyperborea fronds (a) and stipes (b). Data replotted from:

■, Black and Dewar (1949); ▼, Black (1950a);

and from Haug and Jensen (1954) and Jensen and Haug (1956):

◆, Reine; ▲, Vardö; ●, Espevaer.

TABLE X

Inorganic constituents of L. hyperborea, in percentage of dry matter
(Jensen, unpublished)

	Frond		Stipe	
	Autumn	Spring	Autumn	Spring
I	0.3	0.6	0.6	0.8
K	-	8.4	-	11.1
Na	-	3.2	-	1.6
Ca	-	1.4	-	1.7
Mg	-	0.8	-	0.6
Fe	0.03	0.028	0.018	0.01
SO_4	-	4.6	-	2.7
PO_4	-	0.6	-	0.5
Cl	-	8.8	-	11.7
Br	-	0.1	-	0.1
Cu	0.001	0.002	0.002	-
Zn	0.012	0.02	0.012	-

TABLE XI

Trace elements found in L. hyperborea fronds, in mg/kg of dry matter

	Ag	As	Ba	Co	Cr	Cu	Fe	Li	Mn	Mo
Black and Mitchell (1952):	0.5		52	0.39	1.3	15	223	5	23	0.33
Lunde (1970):		63		0.14		10	104		5	0.5
Jensen (Table X)						15				
	Ni	Pb	Rb	Sb	Se	Sn	Sr	Ti	V	Zn
Black and Mitchell (1952):	1.7	16	190			1.0	2600	16	1.1	110
Lunde (1970):				0.09	0.05					78
Jensen (Table X):										160

7.3 Organic constituents

7.31 Carbohydrates

The main carbohydrates of both fronds and stipe of L. hyperborea are (in order of abundance) alginic acid, laminaran, mannitol, cellulose and fucoidan.

The simplest, mannitol, is a fairly early photosynthetic product in Phaeophyceae and may be the main respiratory substrate as has been shown to be likely in Fucus (Percival and McDowell, 1967, p. 22). It is a storage carbohydrate. The seasonal variation in mannitol as percentage of dry matter in fronds and stipes of L. hyperborea from several sites in Norway is shown in Figure 16a and b (Haug and Jensen, 1954; Jensen and Haug, 1956). There is clearly a marked seasonal change in fronds with a sudden rise in response to the best months for irradiance, and a slow decline in the winter when respiration probably exceeds photosynthesis. The seasonal variation in the stipes, where mannitol levels are lower, is distinct but much less pronounced. Black (1948b) was the first to observe these seasonal variations and the frond and stipe differences and his later results (Black and Dewar, 1949; Black, 1950a, 1955b, Table II, Fig. 2) are in agreement with those in Figure 16, though higher mannitol levels in fronds were recorded. Methods for the isolation of mannitol from dry or wet Laminaria are described in Black, Dewar and Woodward (1951).

The polysaccharide laminaran (previously called laminarin) is a hot water-soluble, mainly 1,3-β-linked polyglucan. Its properties and constitution have been investigated by several authors (Connel et al. 1950; Black, Cornhill, Dewar and Woodward, 1951; Black and Dewar, 1954; Friedlaender et al., 1954; Anderson et al., 1958; Annan et al., 1965a, 1965b; Fleming et al., 1966). There are two forms, the "insoluble" which precipitates spontaneously in cold water and the "soluble" which does not because of more branches in the chains (Fleming and Manners, 1965). Laminaran from L. hyperborea is predominantly insoluble, while that from L. digitata and L. saccharina is mainly soluble. Peat et al., (1958) showed that the insoluble form contained about two percent of mannitol, these units being at the ends of the chains and also that there were some 1,6-β-links between the glucose units. Further work on the structure of laminaran is summarized by Percival and McDowell (1967, pp. 55-65). Its synthetic pathway has not been elucidated but there is a suggestion that mannitol and laminaran are readily interconvertible (Percival and McDowell, 1967, p. 20). It is a reserve material common in Phaeophyceae. The seasonal variation in laminaran, in plants from the same source as analysed for mannitol, is shown for fronds and stipes respectively in Figure 16b and c. Here the variation in the fronds is even more marked, though the summer rise comes later than in mannitol. Thus as a reserve it is laid down later than mannitol and probably depleted later. Black (1950c) found that during the period that the laminaran content of the frond is high there is a decrease in the amount of this substance with the depth of occurrence of the plant. A method to isolate glucose from L. hyperborea has been described by Black et al. (1953, 1955).

Fucoidan is composed of sulphated fucose units. In the Phaeophyceae it may be associated with resistance to desiccation, being highly hygroscopic, and is low in Laminaria, being less than four percent of the dry matter (Black, 1954a). Black found that it was higher in the frond than in the stipe and in both showed a seasonal variation similar to that of mannitol. It may, therefore, be another but minor storage substance in L. hyperborea. The isolation and purification is described by Percival and Ross (1950)

It should be noted here that all the storage compounds in this species show a similar, though not identical, variation with season in the frond. Where the new and old fronds have been separated (Haug and Jensen, 1954, Fig. 7) mannitol and laminaran in the old frond decline steadily to nearly zero between February and June while the levels in the new frond remain steady and climb rapidly after June. Because storage materials are at relatively low levels in the stipe and vary little with season, it appears that this part of the plant does not function as the main storage organ. Both these observations fit well with Lüning's (1970a) observations that much of the early growth of the new frond is dependent on the presence of the old frond but not of the stipe (see 2.41). The old frond is thus the storage organ.

Alginic acid is a polyuronide peculiar to the Phaeophyceae. It is composed of D-mannuronic and L-guluronic acid units and Haug (1964) showed that it is a mixture of heteropolymers of these, the proportions varying between alginates from different sources, for example the new and old frond of L. hyperborea (Haug et al., 1969) and between stipes from different sites. Ion exchange and acidic properties were shown to depend on these proportions (Haug, 1964). Quite a lot is known of the synthetic pathway of this substance and this is outlined by Percival and McDowell (1967, pp. 17-19). It is likely that the pathway differs from that of mannitol. Alginic acid mainly occurs in intercellular spaces but is also present as a major component on cell walls, being situated in the middle lamella and the primary membrane, outside the cellulose (Anderson, 1956). Anderson showed that the

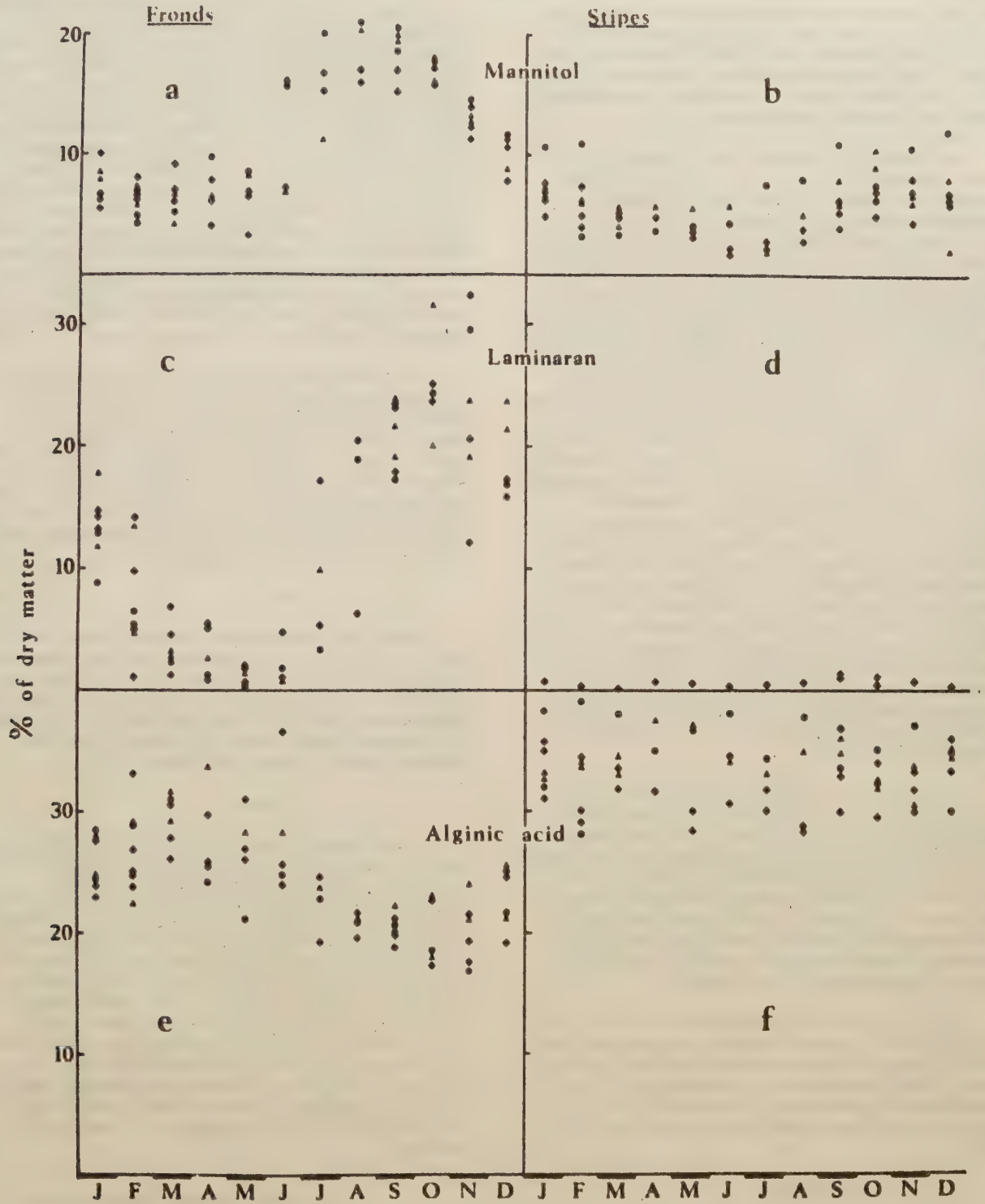


Fig. 16 Mannitol (a, b), laminaran (c, d) and alginic acid (e, f) expressed as a percentage of dry matter in L. hyperborea fronds (a, c, e) and stipes (b, d, f). Data replotted from Haug and Jensen (1954) and Jensen and Haug (1956).

◆, Reine; ▲, Vardø; ●, Espevaer.

proportion of alginic acid increased toward the centre of the tissue of Laminaria, the thick walls of the medulla thus mainly consisting of alginic acid rather than cellulose. Larson and Haug (1961) also found an increase in alginate toward the centre of the stipe.

The levels of alginic acid found at different seasons in fronds and stipes in Norway from the same sites as analysed for mannitol and laminaran are shown in Figure 16e and f. There is clearly a marked seasonal variation in the frond, varying from around 20 percent of the dry matter in autumn to 30 percent in spring. The stipes, however, show no seasonal variation but a higher alginate content of about 30 to 37 percent of dry matter. Black and Dewar (1949) and Black (1950a) observed much lower values for alginic acid of 8 to 10 percent of dry matter in the fronds and 19 to 23 percent in the stipes. The seasonal variation in alginic acid shown by the fronds can be considered as a reflection of the seasonal variation in the storage compounds mannitol and laminaran because all are expressed as a percentage of dry weight. When frond alginic acid is expressed as a percentage of fresh weight (Jensen and Haug, 1956, Fig. 13) this pattern disappears and alginic acid shows a maximum in December and a minimum in June, which may or may not be significant. As there is little variation in storage compounds in the stipe and their levels are low, alginic acid varies little with season and its percentage is correspondingly high. The viscosity of sodium alginate from frond and stipe respectively and after different treatments was investigated by Black et al. (1952).

Cellulose, consisting of 1,4-β-linked glucose units and similar to the higher plant substance (Percival and Ross, 1949) is present in the cell walls of L. hyperborea in much smaller quantities than alginic acid. Black (1950b) observed the seasonal variation in the frond and stipe. It varied in the frond from about four percent of the dry matter to nearly six percent. In the stipe the levels varied from eight to ten percent of dry matter.

Enzymes capable of decomposing insoluble laminaran are produced by many micro-organisms such as those of the microflora of the bovine rumen. The decomposition of alginates is not so widespread a phenomenon. Laminarate and an alginate have been isolated (Chosters et al., 1956).

7.32 Proteins

The protein content of brown algae is generally quite low and that of L. hyperborea is no exception. There is a seasonal variation in the protein content of fronds from about five percent of the dry weight around August to 13 to 15 percent around April, though 20 percent has been recorded in new fronds at that time (Haug and Jensen, 1954; Jensen and Haug, 1956). This seasonal variation (also reported by Black and Dewar, 1949 and Black, 1950a) is similar to that of alginic acid and presumably also reflects the variation in storage polysaccharides making up the bulk of the dry weight in late summer. Thus, when expressed as a percentage of fresh weight, frond protein varied from one percent in June to two percent in December (Jensen and Haug, 1956), a cycle similar to that of alginic acid again. The protein content of the stipes varies little with season and usually lies between 7 and 12 percent of the dry matter (Black, 1950a; Haug and Jensen, 1954; Jensen and Haug, 1956).

Although most of the nitrogenous matter in L. hyperborea is in the form of proteins and peptides, some free α-amino acids have been found, mainly alanine, aspartic and glutamic acids (Channing and Young, 1953). The amino-acid composition of isolated bulk proteins from L. hyperborea fronds were analysed by Coulson (1955). Coulson (1953) observed a seasonal variation in cysteic acid content from nil in September to a maximum between May and August.

7.33 Fat

The ether-extractable matter (total fat) is low in all Laminaria species. In the fronds of L. hyperborea it varies from about 0.5 to 1.5 percent of the dry matter, usually being low in August and high in the spring while in the stipes it differs little from 0.5 percent (Haug and Jensen, 1954; Jensen and Haug, 1956).

7.34 Pigments

The Phaeophyceae contain chlorophylls a and c, fucoxanthin, violaxanthin and β-carotene (Jensen, 1966). Seybold and Egle (1938) analysed L. hyperborea and found 2 320 mg of chlorophyll, 85 mg β-carotene, 469 mg fucoxanthin and 45 mg "xanthophyll" per kilogramme of dry matter. Owen (1954) made determinations of frond and stipe material, fresh or previously dried, but all his figures are considerably lower than those of Seybold and Egle. His values for L. digitata are similarly much lower than those of both Seybold and Egle and of Jensen (1966), who did not make determinations on L. hyperborea. Jensen found a level for violaxanthin in L. digitata of 110 mg/kg dry matter.

7.35 Other organic constituents

A number of vitamins have been shown to occur in L. hyperborea. Vitamin A which in this case only occurs in the form of its pro-vitamin β-carotene, is dealt with in the previous section. Of the vitamin B group

the niacin content of this species was investigated by Larsen (1958) over a period of six years. There was a remarkably consistent seasonal variation in the fronds from about 10 mg/kg dry matter in October to about 35 mg/kg in April and a single year's observations on the levels in the stipe indicated a similar cycle. A similar but much less regular seasonal variation was observed in the biotin content of the fronds, varying from about 0.3 to 0.5 mg/kg of dry matter (Larsen, 1961). Karlström (1963) measured the vitamin B_{12} content of L. hyperborea and found 0.04 mg/kg of dry matter, but Ericson (1953) found up to 1 mg/kg in L. saccharina. Ericson also found vitamins B_1, B_2, folic and folinic acid in L. saccharina. Lunde and Lie (1938) found vitamin C levels of 100-470 mg/kg wet weight of L. hyperborea which should correspond to about 700 to 3 400 mg/kg dry matter. The maximum was in April. Rönnerstrand (1943) found 70 mg/kg wet weight in summer, corresponding to about 350 mg/kg dry weight. Of the vitamin E group only α-tocopherol has been found, in small but consistent quantities of 10 to 30 mg/kg of dry matter (Brown, 1953; Jensen, 1969).

Fucosterol, the typical steroid of brown algae, occurs in L. hyperborea as approximately 0.1 percent of the dry matter (Black and Cornhill 1951).

Auxins have been detected in this species, in chromatogram spots close to but possibly not identical with indolylacetic acid and indolylacetonitrile (Mowat, 1964).

8 UTILIZATION

8.1 Human food

This species is used very little as human food. In the past, in times of starvation, the frond has been eaten in Iceland (Hallsson, 1964).

8.2 Animal fodder

There is similarly little use for L. hyperborea as animal food though cattle occasionally eat cast plants on the shore.

There have been many experiments on the use of dried seaweed meal as a supplement to the diet of domestic animals and although most of the meal used for this is prepared from Ascophyllum nodosum (see Baardseth, 1970) some experiments have included L. hyperborea meal. For example, Hand (1953), Black (1954b) and Hand and Tyler (1955) found that replacing ten percent of the normal diet of egg-laying hens with L. hyperborea meal (preferably prepared from fronds) had no harmful effect (though water consumption went up), but did not appear to have an advantage in an already balanced diet. On the other hand, Høie and Sandvik (1956) showed that L. hyperborea meal added to a diet not supplemented with yeast, grass meal or cod liver oil stimulated a marked improvement in the growth and health of chicks. Particularly good results were obtained from meal prepared from young fronds. However, an addition of five percent L. hyperborea meal to an all-round basal diet for chicks, although doing no harm, had no beneficial effect (Høie and Sannan, 1958). Ten or 15 percent additions were in fact unfavourable. Similarly the addition of ten percent L. hyperborea meal to the diet of dairy cows had no effect on milk production (Burt et al., 1954). Black and Woodward (1957), from theoretical considerations, concluded that seaweed meal (including that from L. hyperborea), supplied as ten percent of the diet, could provide enough NaCl and I_2, in addition to Cu, Co, Mn, Fe and other possible trace elements and vitamins for the normal requirements of all farm livestock.

Sunde (1956) found that when laying hens were given seven percent of their feed as L. hyperborea meal the I_2 content of the eggs was 150 times that of those fed on the usual diet.

Although the use of seaweed meal in livestock feeding has many advantages (Baardseth, 1970), that from L. hyperborea has too high an iodine content to be of general use and is not sold for this purpse.

Preservation by ensiling has been studied (Black 1955a).

8.3 Manure

Seaweed has been used as manure by coastal farmers for centuries. L. hyperborea is particularly useful in some areas because large quantities are washed ashore at times. It is still used occasionally in this way in Scotland and other places though generally other forms of fertilizer have taken its place.

Seaweed meal or liquid fertilizers have a great many applications and advantageous side effects (Booth, 1966) but again these are prepared mainly (in Europe) from Ascophyllum and not L. hyperborea. Some liquid fertilizer is manufactured from L. hyperborea fronds in Britain, however. An example of an experiment involving the use of this species as fertilizer is that by Myklestad (1964). It was found that, as a supplement to basic fertilizing of newly cultivated ground, seaweed stimulated an increase in turnip production which was greater than could be attributed to the provision of N, K and P. On soils in good condition, however, it had little effect.

8.4 Industrial products

The earliest industrial application for this species was in the production of "kelp". This originally meant the ash from burnt seaweed. This was used as a source of soda, particularly for the glass industry (Chapman, 1970). Soon after alternative sources were found for this, early in the nineteenth century, the ash was used instead as a source of iodine and this continued for about a century in Scotland. In France, however, it continued for longer (Feldmann, 1953) but ceased in 1958 (Chapman, 1970).

Most of the L. hyperborea now collected for commercial purposes in Norway and Britain is used for the manufacture of alginates. This species is little used by alginate industries in other countries. In Britain about one third of the alginate produced originates from L. hyperborea. The British industry (Alginate Industries Ltd., London) uses air-dried stipes while the Norwegian factory (Protan & Fagertun A/S, Drammen) utilizes the whole plant, undried. The alginic acid is extracted from the algal material with base, precipitated as free acid and neutralized to sodium alginate which is the main product. Alginic acid and its salts, the alginates, find very many applications in pharmaceutical and food industries and in printing and paper sizing processes (see Chapman, 1970).

There has been quite a lot of work on the use of the polysaccharide laminaran in medicine. The insoluble form can be most economically isolated from L. hyperborea fronds between August and December (Reid, 1956). It can act as

an anti-coagulant after being sulphated (Dewar, 1956). With about 0.6 sulphate groups per glucose molecule this laminaran can act as an anti-lipaemic agent (Besterman and Evans, 1957). However, some laminaran sulphates have been found to have harmful effects (Adams and Thorpe, 1957; Adams et al., 1958). Although laminaran has advantages as a talcum powder substitute, the insoluble form (economically produced from L. hyperborea only) was found to affect liver and kidney tissue of test animals and its use was abandoned (Blaine, 1951).

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SYNOPSIS OF FISHERIES BIOLOGICAL DATA

This is one of a series of documents issued by FAO, CSIRO and USFWS concerning species and stocks of aquatic organisms of present or potential economic interest. The primary purpose of this series is to make existing information readily available to fishery scientists according to a standard pattern, and by so doing also to draw attention to gaps in knowledge. It is hoped that synopses in this series will be useful to other scientists initiating investigations of the species concerned or of related ones, as a means of exchange of knowledge among those already working on the species, and as the basis for comparative study of fisheries resources. They will be brought up to date from time to time as further information becomes available either as revisions of the entire document or their specific chapters.

The relevant series of documents are:

FAO	**Fisheries Synopsis No.**	FR/S
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	and	
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* FIRM/S104	Synopsis of biological data on the penaeid prawn *Metapenaeus monoceros* (Fabricius, 1798)	October 1970
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* Published in the Proceedings of the World Scientific Conference on the Biology and Culture of Shrimps and Prawns, Mexico, 12 to 21 June 1967.

MI/C3845/2.72/E/1/900